Mortality of Migratory Barren-ground Caribou on the Calving Ground of the Beverly Herd

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MORTALITY OF MIGRATORY BARREN-GROUND CARIBOU ON THE CALVING GROUND OF THE BEVERLY HERD, DISTRICT OF KEEWATIN, NORTHWEST TERRITORIES, 1981-83

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EXECUTIVE SUMMARY

The Beverly herd of migratory barren-ground caribou (Rangifer tarandus groenlandicus) has declined in numbers throughout the 1970s into the 1980s. In practice, the management of caribou is limited to the management of hunting and predation. To manage migratory barren-ground caribou for sustained annual harvest, sources of caribou mortality other than hunting have to be measured and evaluated. Therefore, we investigated the causes of mortality of newborn caribou calves of the Beverly caribou herd to evaluate the importance of predation during the calving and early postcalving and provide management recommendations. The following is a report of our findings over a 3-year period (1981-83).

We searched during low-level helicopter flights for dead calves on the Beverly caribou herd calving ground in the District of Keewatin, Northwest Territories during calving and early postcalving periods in 1981, 1982 and 1983. The areas searched in all 3 years were similar and encompassed the core of the calving ground in each year.

The breeding cows and their juvenile followers arrived on an essentially snow covered calving ground by the third week of May and most calving took place during the first 2 weeks of June in all 3 years. In 1981, calving peaked earlier (2-5 June) on the high density eastern section compared to a peak of 7-9 June by the lower density of cows on the southwest section of the calving ground. Again in 1982, calving peaked earlier (9-10 June) on the high density central portion and later (11-12 June) on the medium density eastern section of the calving ground. In 1983, no regional differences in the peak of calving were discerned, 8-14 June. In 1983 the relative densities of breeding cows was distributed about as in 1982 though the high density area was further south to the north end of Sand Lake. The general impression of the distribution of the cows was that the highest density area moved progressively southwest from the Deep Rose Lake area in 1981 to the north end and northeast side of Sand Lake in 1983.

Two hundred and eighty-seven dead or incapacitated newborn caribou calves were found and necropsied between 31 May and 20 June 1981, 8-23 June 1982, and 6-17 June 1983. The causes of death were determined with certainty for 225 of the calves: 154, wolf (Canis lupus) predation; 1, grizzly bear (Ursus arctos) predation; 14, fetal atelectasis (stillbirths); 18, neonatal atelectasis (premature births or in utero complications); 14, separation or abandonment (malnutrition/ starvation complex); 15, patho-physiological disorders; and 9, pneumonia. Thirty-two calves were classified as suspect cases: 19, wolf predation; and 13, fetal or neonatal atelectasis. The cause(s) of death could not be determined for the remaining 30 calves.

Patho-physiological disorders included (1) drowning, shock, or stress while entrapped in near freezing water or slush; (2)

intraspecific trauma such as being kicked or stepped on by a maternal or strange cow; (3) malnutrition/starvation after incapacitating injury (broken hind leg); (4) malnutrition/starvation due to maternal cow's death; (5) hydrocephalus; (6) parrot mouth; and (7) ruptured liver.

In the overall 3-year sample of 287 calves, 42.9% were males, 35.9% were females, and the sex of 21.2% was undeterminable. Statistical analysis of the occurrence of calves by sex in the samples suggests that calves were not predisposed to death because of their sex. Almost all (97.6%) of the calves were estimated to be less than 1-week-old at death and most (77.0%) were less than 4 days of age, suggesting that relatively more calves died during the first 3 days of life than during the subsequent 4-7 days of life.

Wolf predation is the most important and the only readily manageable cause of early calf mortality. Newborn (<7 d) caribou calves are exceptionally easily caught and killed by wolves and we observed 'surplus killing' (no utilization of carcass); 'excessive killing' (only slight utilization of carcass); and 'specialized feeding' (apparent preferences for milk curds and viscera over muscle tissue) by wolves. Consequently, previously established estimates of numbers of caribou annually required by wolves cannot be used to evaluate the impact of wolves on newborn calves as the low rate of utilization was not included in the early estimates. As only 12.8% of all wolf-killed calves may have died from other causes had they not been killed by wolves compensatory mortality was a minor consideration in our evaluation of wolf predation on newborn caribou calves.

Helicopter searches for dead calves should be routinely carried out as an extension of the aerial survey program on the calving grounds which use helicopters to obtain calf/cow counts. The monitoring of causes of death of newborn calves would detect any anomalies or catastrophic events during calving. Additionally, detailed records of predator sightings should be routinely recorded as past information on predators on the calving grounds in various years has been too poorly reported to be useful.

Future studies of early caribou calf mortality would be facilitated by: (a) radio-collared calves to describe the chronology of calf mortality, and for comparison with the sample of unmarked dead calves; (b) radio-collared pregnant cows to additionally evaluate reproductive rates and calf mortality; (c) systematic aerial and ground surveys of the calving ground from precalving through calving into early postcalving to determine distributions and size of the breeding segment and calf production and survival; and (d) extensive, systematic helicopter searches for dead calves and cows on the core of the calving ground from precalving, calving through to early postcalving.

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INTRODUCTION

This 3-year study was initiated in 1981 in response to concerns over the decline of migratory barren-ground caribou (Rangifer tarandus groenlandicus) of the Beverly herd during the 1970s. The Beverly and Kaminuriak Caribou Management Board represents the federal, provincial, and territorial governments together with the native users of those two caribou herds. The Board was established to direct and advise on management of the caribou at a time when the herds were believed to be declining and action was necessary to halt or at least stabilize the decline. Management of caribou is, in practice, limited to managing predation and the harvest (e.g. Bergerud 1974a), but too little was known about the causes and extent of natural mortality in the Beverly herd to consider initiating any management of predation or harvest. The Beverly herd's calving grounds have also been an area of mineral exploration and our study contributes baseline knowledge in the event of continued exploration or development of ore bodies.

Natural mortality is the least understood aspect of caribou management because of the difficulties of quantifying it. The natural mortality of calves until they are 1-yr-old is of particular concern to wildlife managers not only because it is frequently high (e.g., Kelsall 1968, Skoog 1968), but because the number of 1-yr-old calves is an essential part of the measure of the potential maximum that a herd can increase in numbers.

Since 1978 to 1980, the Northwest Territories (NWT) Wildlife Service[1] has biannually monitored calf survival by obtaining the ratio of calves to cows in the fall and late winter. In cooperation with our study of calf mortality the monitoring of calf survival was intensified by greater sampling effort in 1981 and 1982 (Gunn, unpubl. data).

We concentrated on describing the causes of mortality of newborn calves on the calving ground because they had not been previously described for the Beverly herd though observations indicated the extent of calf mortality was extensive in some years (Heard and Decker 1980). Cows and their newborn calves are concentrated on the traditional calving grounds so visual searches for calf carcasses are feasible (Miller and Broughton 1974). Once the carcasses were located, the cause of death was determined during postmortem examinations. Radiotelementry has been used in studies of mortality of newborn caribou (in Alaska (Mauer et al. 1983, Whitten et al. 1984)) to locate carcasses of previously radio-collared calves but many hunters of the Beverly herd are culturally opposed to the capture and marking of caribou. Additionally, the Alaskan calves were radio-collared when a few days old which results in an under-estimate of some mortality factors such as stillbirth and premature births. As we wanted to avoid such biases in our study, we relied on visual searches for carcasses.

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In our report, we describe the evidence for the causes of mortality of caribou on their calving ground at or about the time of calving. We evaluate the management implications of our results and develop three recommendations for the caribou managers.

Our findings were generally similar to those in the only other directly comparable study of calf mortality of barren-ground caribou in that wolf (*Canis lupus*) predation was the most frequent cause of calf mortality (Miller and Broughton 1974).

STUDY AREA

1. Calving Ground, 1981-83

Our study area is the northern portion of the Beverly calving grounds that have been used during the 14 years between 1957 and 1983 for which there are data (Fleck and Gunn 1982, and this report), (Figs. 1 and 2). The characteristics of the topography, snowmelt patterns and vegetation have been compiled for the calving grounds north and south of Beverly Lake (Fleck and Gunn 1982).

Glacial landforms dominate the rolling topography which has a local relief of less than 60 m. Drainage patterns are poorly developed on the flat-lying sandstone beds that cover the Precambrian Shield. The shield contributes to the rugged landscape in the northeast corner as gneissic granitic outcrops. The sandstones form low scattered outcrops in the southern and western parts of the calving grounds.

Four dominant glacial landforms contribute to the varied topography that is characteristic of the calving grounds compared to the surrounding areas (Fleck and Gunn 1982). Much of the area is fields of drumlins and lines of eskers orientated northwest-southeast. North of Sand Lake is a flat extensive outwash sand deposit which also extends southeast to the north end of "Sandhills" Lake. West of Deep Rose Lake is a smaller outwash sand deposit and a glacial till plain studded with boulders. Boulders are also characteristic of the surfaces of the drumlins as most all the glacial till is rich in boulders.

Fleck and Gunn (1982) initially classified five vegetative communities based on similar percentages of structural forms for the northern Beverly calving grounds (lichen, dwarf shrub, tussock-short sedge, tussock-moss, and tall sedge-moss). The xeric and mesic drumlin and esker tops and sandy areas are dominated by lichen communities. Graminoids and mosses dominate the more hydric lowlands. Jingfors *et al.* (1982) reclassified the vegetative communities using topography, moisture regimes and landforms into four range types to determine the preferential use by cows and calves: lichen uplands, dwarf shrub, meadow, and rock/sand barrens.

The green and black colours that are so characteristic of the calving grounds are from the thick lichen mats of *Cornicularia divergens* and *Alectoria ochroleuca* which are the dominant species of the lichen upland range type. Other lichen species and prostrate shrubs including *Ledum decumbens*, *Vaccinium vitis-idaea* and *Empetrum nigrum* also occur on lichen uplands which is the most extensive range type (Jingfors *et al.* 1982). Lichen uplands cover 38.8% of the calving grounds being found on drumlins, eskers and sandy areas.

Lichen uplands merge on lower slopes into the dwarf shrub range type. The dwarf shrubs *Salix* spp. and *Betula glandulosa* are the dominant species in the dwarf shrub range type which covers 24.1% of the northern calving grounds. The lichens *Cornicularia divergens*, Cetraria nivalis and Alectoria ochroleuca are also important species as are moss and Carex spp.

The surface water of the numerous lakes and ponds account for 20.8% of the surface area. The bases of the drumlin and esker slopes and other hydric areas are tall sedge meadows dominated by Carex spp. and tussock meadows dominated by Eriophorum vaginatum. The meadow range type accounted for only 12.3% of the surface area and rock/sand barrens range type covered the remaining 4.0% of the surface area (Jingfors et al. 1982). The rock/sand barrens are glacio-fluvial sand deposits sparsely covered by moss and lichens.

The many lakes on the calving grounds are studded with small islands and characteristically have irregular outlines with long peninsulas. The dominant range type was subjectively determined to be lichen uplands. The cows concentrated onto those areas during and just after calving.

The selection of the meadow range type by foraging caribou during calving and postcalving despite its relatively low occurrence can be understood from the phenology of the plants, which is tracked by the caribou (Jingfors et al. 1982, Gunn et al. 1983). When the cows arrive on the calving grounds in late May the ground is snow covered except for the tops of some ridges. In early June, the lichen uplands and rock/sand barrens become snow-free exposing the fruticose lichens but phenological development is relatively slow as for example; the dominant rush Luzula confusa does not start greening until the third week of June. In the meadows, however, greening of the graminoids starts even while the roots and lower stems are still frozen in the ground. As the tussocks of Eriophorum vaginatum emerge from the snow in early June, the plants have new green growth of floral heads and leaves. The preference of the caribou for the greening plant tissue explains the selection of the meadow range type by foraging caribou during calving (2-9 June) and postcalving (11-23 June) in 1982 (Jingfors et al. 1982). Caribou bedded in both lichen upland and meadows during early June but as the melt progressed and the depth of standing water increased on the meadows, the caribou preferentially bedded on the drier upland lichens during postcalving.

2. Weather, June 1981-83

The meterological data collected (Section 1., Methods and Materials) suggest that the weather during calving and early postcalving was mostly favourable to the survival of newborn calves in all 3 years of the study (Table 1, Fig. 3-7, and App. 1). Temperatures were seasonally moderate to mild, for the most part; precipitation was seasonally light with three exceptions in 1981 and two in 1982; and winds mostly were seasonally moderate to light.

During the 3 years of this study daily maximum temperatures averaged highest in June 1981 and lowest in June 1982 (Fig. 3). In 1981 and 1983 daily minimum temperatures were similar and paralleled each other throughout the first 3 weeks of June (Fig. 4). In June 1982 daily minimum temperatures showed more variation and most often remained lower during the same time period than in 1981 or 1983 (Fig. 4). Temperatures were markedly higher in the first week of June 1981 than during the same week in 1983 and even more so than in 1982 (Fig. 5). As a result, vegetation greened earliest in June 1981 and latest in June 1982.

The relative lack of precipitation during the peak of calving in the first week of June in all 3 years apparently was beneficial to the survival of newborn calves (Table 1). The potentially lethal combination of precipitation, strong winds, and relatively low temperatures during the calving periods appeared most severe on 10 and 11 June in both 1981 and 1982; and only on 4 June in 1983 (Table 1). The most severe day during the first week of postcalving in all 3 years was 19 June 1982, when strong winds were associated with the heaviest rainfall at relatively low temperatures (Table 1). The only other apparent severe day during early postcalving was on 16 June 1981, when the second heaviest rainfall occurred (Table 1).

Winds in the strong-class (30^{+} km · h^{-1}) were recorded slightly more in 1983 than in 1982 or 1981 but in all 3 years were less than 20% of all winds recorded (Fig. 6). In 1981 winds were most frequently out of the northeast, but in 1982 and 1983 they were most commonly out of the north (Fig. 7). In 1981 all winds recorded in the strong-class were out of the eastern quadrants, only 40% were in 1982, and none were in 1983. In 1982 40% of the winds recorded were out of the south and 20% were out of the north. In 1983 62.5% of the winds recorded in the strong-class were out of the northwest, 25% were out of the north, and 12.5% were out of the south.

METHODS AND MATERIAL

1. Field

In 1981-83 we flew nonsystematic searches in a Bell-206B turbo-helicopter at about 10 to 30 m above ground level (agl) at speeds of 90 to 160 km/h for dead caribou. Three observers usually rode with the pilot during searches, but sometimes, only two observers accompanied the pilot. The helicopter and base camp were shared in 1981 and 1982 with another project crew and the sharing of the helicopter and prevailing weather in all 3 years often influenced the timing and area of some searches.

The study design called for us to locate large numbers of cows and recently born calves as well as groups of maternal cows and their calves during early postcalving. We overflew cows during calving, when they were relatively scattered. Once the cows and their newborn calves had left we returned to those areas and searched more intensively. We also flew along the peripheries of large aggregations of caribou throughout the study period.

When we searched a particular area, the helicopter was flown back and forth across the area so that sections searched were completely overlapped on each successive pass.

We recorded all sightings of wolves, grizzly bears (*Ursus arctos*), arctic foxes (*Alcpex lagopus*), herring gulls (*Larus argentatus*), glaucous gulls (*L. hyperboreus*), rough-legged hawks (*Buteo lagopus*), parasitic jaegers (*Stercorarius parasiticus*), long-tailed jaegers (*S. longicaudus*), pomarine jaegers (*S. pomarinus*), golden eagles (*Aquila chrysaetos*), and ravens (*Corvus corax*).

We performed detailed field necropsies on the caribou carcasses. All data were recorded on a field form: the 1981 form was redesigned in 1982 to allow a more detailed, quantitative record of each case. We numbered each carcass and recorded the following data.

(1) The date the carcass was found - day/month/year.
(2) The location of the carcass by latitude and longitude to the nearest minute - determined from 1:250 000 Geological Survey of Canada topographic maps.
(3) The sex of each carcass was determined by examination of genitalia; heavily utilized carcasses of undeterminable sex were listed as unknowns.
(4) Age was estimated by a combination of subjective and objective variables (see Table 2).
(5) The weight was recorded in kilograms as 'whole' or 'partial'.
(6) The numbers and kinds of all other animals present at or nearby the death site were recorded.
(7) The parts of the carcass that were partially or wholly missing as a result of predation or scavenging were recorded: tongue, eye(s), head, neck, lungs, heart, liver, stomach (milk curds), kidneys, intestinal tract, flank, hindquarters, forequarters, back, rump, hind leg and foreleg.

(8) Wounds on the skull, head, neck, back, flank, chest, abdomen, hind legs, forelegs, or other (specific) were recorded as punctures, hemorrhages or traumas.

(9) The right diaphragmatic, left diaphragmatic and apical lobes of the lungs were recorded by percentage as normal or with atelectasis, or pneumonia.

(10) Stomach contents were recorded as 'empty'; milk curds only; milk curds and some little vegetation; milk curds, well mixed with vegetation; and vegetation only.

(11) The fourth mandibular premolar (pm4) was checked for state of eruption, presence or absence of staining and for vegetation impacted in the infundibula.

(12) We noted whether or not the carcass had been fed on by predators or by scavengers and the types and locations of entry holes to the body cavities.

(13) We then listed all remarks and described any conditions that were pertinent to the case.

We used maximum-minimum thermometers at the base camp to record daily highs and lows at ground level (hung 0.3 m above ground level, and shaded from above but open to surrounding air circulation). We also had a Glaisher's 20.3 cm bucket-type rain gauge at the base camp in 1981 and 1982 for recording daily precipitation. Twice daily at about 0800 and 2000 we recorded temperature; estimated wind speed as calm (0-1 km $\cdot$ h^{-1}), mild (2-9 km $\cdot$ h^{-1}), moderate (10-29 km $\cdot$ h^{-1}) and strong (30+ km $\cdot$ h^{-1}); recorded wind direction by the eight major points of the compass; described type and intensity of precipitation; and recorded cloud cover.

We estimated the ages of all caribou, except calves, by examination of the eruption and attrition (wear) patterns of their mandibular teeth (Miller 1972, 1974). We used the following criteria for estimating ages 1, 2, 3, and 3+ years.

At 12 to 13 months of age all mandibular premolars (p2, p3, p4) are still deciduous (milk) teeth. The deciduous p4 is the diagnostic tooth, as it is sexitubercular (has three pairs of cusps). The additional pair of cusps makes the deciduous p4 longer and recognizable from its permanent counterpart which is only quadritubercular (has only two pairs of cusps). Also, the third mandibular molar (m3) is absent at 12 to 13 months of age.

At 24 to 25 months of age the mandibular premolars can still be deciduous, permanent and erupting, or permanent and fully in place; and the m3 is either erupting or mostly in place (appears erupted, but is not completely so). If the premolars are permanent, they are lightly stained and easily recognizable. Also, the crests and crescents of p3 and p4 are only slightly worn and those of p2 are not worn at all. The m3 is the diagnostic tooth as its additional, single, distal cusp is not fully erupted and staining is lacking on the posterior portion of m3. Also, if in doubt, the closure patterns of the apices of the roots of p4 and m3 can be examined: at 24 to 25 months the apices are most all open, at 36 months they are all closed.

At 36 to 37 months the mandibular tooth row is fully developed and some wear has occurred. However, the distal cusp of the m3 has only moderate to no wear. The diagnostic characteristic is associated with the distal cusp of the m3: the gum line around the distal cusp has not retracted sufficiently to expose the full height of the cusp. This condition pertains because the lower jaw has not completely elongated at 36 months of age (Watson and Keough 1954, Miller 1974).

From 4 years of age onward the estimates of age based on examination of the mandibular wear patterns are clumped into 2-year age classes: 4-5, 5-6, 6-7, 7-8, 8-9, and 9-10+. This clumping reflects the variation in individual wear patterns of the mandibular teeth (see Miller 1974 for detailed descriptions and photographs of mandibular tooth rows of caribou 4 to 10+ years of age). Similar age classification schemes were given for Alaskan caribou (_R_. _t_. _granti_) by Chatelain (1954), Watson and Keough (1954), and Skoog (1956, 1968).

2. Diagnoses and Analyses

2.1 Determining cause of death

The location and overall appearance of each death site, and the general external appearance of each carcass were considered as possible initial evidence to be used in our determination of the cause of each death. The above information was primarily used in assigning causes of death to suspect cases.

When a carcass was spotted, we landed and searched the immediate area on foot. At the site of each carcass we recorded the presence of other animals: maternal cow, and avian or mammalian predators or scavengers. We also recorded the posture of the carcass, noting whether or not it was in a natural resting position; the presence of scuffed vegetation; and the presence of types of tracks, hair, feathers, and scat.

We noted body temperature, condition of the umbilicus, and extent of rigor mortis before we posted or labelled and bagged the carcass. Calf carcasses were examined on site (1981) or returned to our base camp (1982, 1983). Carcasses of cows were examined on site (with one exception that was slung by helicopter back to the base camp).

Each carcass was first examined externally and aged; then weighed with a heavy duty straight spring balance to the nearest 0.25 kg.

Each carcass was then skinned and the contents of the body cavities removed for examination. General condition of body tissues (colour, consistency, softness, etc.); post-mortem imbibition on mesentery or omentum; imbibition of bile on liver; firmness of kidneys; presence, colour, and clotting of blood in heart (together with other conditions of the carcass when found) were noted to estimate approximate time of death. An examination was made for evidence of trauma associated with predation, trauma from other causes, pathological conditions, and physiological disorders.

We established 10 categories of death: (1) wolf predation; (2) suspect wolf predation; (3) grizzly bear predation; (4) fetal atelectasis; (5) neonatal atelectasis; (6) suspect fetal or neonatal atelectasis; (7) separation or abandonment (malnutrition/starvation complex); (8) patho-physiological; (9) pneumonia; and (10) unknowns. For some purposes we lumped the above 10 categories into four major categories: (1) wolf predation; (2) suspect wolf predation; (3) non-predator deaths; and (4) unknowns. Grizzly bear predation was not considered in these four major categories because of its rarity in our study.

2.1.1 Predation

We used type and location of wound(s); occurrence of hemorrhage(s), or frank blood; and tissue trauma induced before death to differentiate predation (wound inflicted on living calf) from scavenging (postmortem tissue damage). In some cases the type of entry into the body cavity also helped to distinguish feeding by wolves from feeding by gulls. 'Wolf predation' was primarily determined by the presence of a crushed, fractured, or canine tooth punctured skull; and secondarily by the criteria stated above in the first sentence, 'Grizzly bear predation' was primarily determined by the carcass remains being cached and covered by soil and litter; or by massive damage to skeletal parts and disarticulation of the head or limbs from the torso (no wolverines [*Gulo gulo*] or lynx [*Lynx canadensis*] were seen nor was any evidence of their presence on the Beverly calving ground obtained during the course of this study). Cases with trauma or hemorrhages but lacking any direct evidence of wounds to critical areas of the body were classified as 'suspect' cases of predation.

Identification of the predator, if not observed making the kill, was made by evaluating the array of evidence from the death site and the carcass, and is aided by descriptions from the literature and empirical observations (e.g., Murie 1948, Thompson 1949, Johnson 1951, Davenport 1953, Spencer 1955, Borg 1962, Harris and Price 1962, Atwell 1964, Sulkava and Rajala 1966, Adorjan and Kolenosky 1969, Mech 1970, Rowley 1970, Cook *et al.* 1971, Ogle 1971, Wiley and Bolen 1971, Alford and Bolen 1972, Cole 1972, Davenport *et al.* 1973, Stephenson and Johnson 1973, White 1973, Miller and Broughton 1974, Bolen 1975, Henne 1975, Mysterud 1975, Nieland 1975, Smith 1975, Van Ballenberghe *et al.* 1975, Bowns 1976, Connolly *et al.* 1976, Roy and Dorrance 1976, Goodwin 1977, Peterson 1977, Timm and Connolly 1977, Buskirk and Gipson 1978, Connolly 1978, Elgmork 1978, Ballard *et al.* 1979, Reynolds 1980, Griffel and Basile 1981, Haynes 1982, Wade and Bowns 1982).

2.1.2 Non-predator deaths

'Fetal atelectasis' was determined by the retention of 100% fetal lung tissue in the thoracic cavity (complete failure of the lung tissue to convert to air breathing neonatal lungs). Secondary evidence for making the diagnosis involved the presence of remnants of afterbirth adhering to the pelage or patches of sticky amniotic fluids on the pelage; total absence of wear on the hooves; and an empty stomach. Fetal atelectic lungs were recognized by their relatively small, purplish (blue-red) appearance. The standard test used for verifying fetal lung tissue was submersion in water: if the tussue sank, it was fetal lung; if the tissue floated, it was distended air breathing neonatal lung.

'Neonatal atelectasis' was determined by the presence of patches of fetal atelectic lung tissue in the only partially distended, air breathing neonatal lungs. Such neonatal atelectic lung tissue appeared as relatively dense, dark purplish blothces of varying sizes in one or more of the lobes of the lungs in contrast to the surrounding distended, lighter pinkish colured air breathing neonatal lung tissue. The atelectic condition of the lung tissue was tested by submersion in water (as for fetal atelectasis). Secondary evidence could include those listed for fetal atelectasis but in some cases the pelages could be clean; the hooves could show some wear; or the stomach could have milk curds in it.

'Suspect fetal or neonatal atelectasis'. A carcass that exhibited an external appearance of a calf with fetal or neonatal atelectasis but lacked any lung tissue for verification of an atelectic condition was classified as a suspect case of fetal or neonatal atlectasis, if no other pathological or physiological disorders could be discerned.

'Separation or abandonment (malnutrition/starvation complex)' was considered the category of death when there was no milk in a stomach but there was vegetation; and no other evidence of any trauma, or pathological or physiological conditions could be discerned; and no maternal cow was present by or near the carcass. The calf was considered to have died from a malnutrition/starvation complex, sometimes involving pneumonia as part of the complex, which was initiated by the calf's separation from or abandonment by its maternal cow.

'Patho-physiological'. Whenever a carcass was diagnosed as having any type of pathological or physiological disorder other than those conditions given specific categories the case was placed in this generalized death category. This was done primarily to better allow subsequent comparisons with other studies.

'Pneumonia'. When a calf had dark mottled pneumonic patches in its lungs; foamy fluid in its trachea; and there was no evidence of separation or abandonment from its maternal cow; or no other evidence of trauma, pathological or physiological conditions that could be the primary cause of death the calf was considered to have died from pneumonia. When a calf showed a malnutrition/starvation/pneumonia complex (the pneumonic condition being minor) it was put in the separation or abandonment (malnutrition/starvation complex) category. Pneumonia was recorded separately from other patho-physiological disorders because it supposedly can be a major cause of death of newborn caribou calves during calving periods with much inclement weather.

2.1.3 Unknowns

When a carcass was too fragmentary, or too decomposed or no evidence was apparent to even suspect the cause of death, the carcass was classified as an 'unknown'. Unknowns were not considered in our quantitative evaluations of the relative importance of the various causes of death of newborn calves.

2.2 Evaluating whole body weight

We arbitrarily choose 4.0 kg as the threshold viable whole body weight of newborn calves in the Beverly herd. Our choice was based mainly on our previous knowledge of calf weights from the Beverly and the Kaminuriak herds (McEwan 1959, Kelsall 1968, Miller and Broughton 1974, Dauphine 1976). Our choice was independent of those made by other workers. Skoog (1968:568) believed that calves weighing less than 3.5 kg had little chance of survival. Weights were recorded in 0.25 kg increments, therefore, any whole body weight of 3.75 kg or less was considered nonviable and any weight of 4.0 kg or more was considered viable.

Calves that were totally intact or those that had only their eye(s) and/or tongue, or less than 0.25 kg of deep muscle tissue or viscera missing were used to calculate average whole body weight and the associated standard error of the mean value on an annual basis.

2.3 Estimating carcass utilization

We used three approaches for estimating carcass utilization of calves by predators or scavengers. Estimates of utilization of individual carcasses on a weight basis were restricted to calves that were <7 d old at death to minimize the influence of individual variation in whole body weight which would increase if calves older than 7 d were included.

One approach involved listing the major parts of the carcass that were missing and assumed to be utilized by predators or scavengers: (1) deep muscle tissue; (2) viscera; (3) tongue; and (4) eye(s). The amounts of deep muscle tissue or viscera missing were then rated as being (1) all, (2) most, or (3) some used. These ratings were based on various combinations of the deep muscle masses or visceral parts that were missing from the individual carcass (App. 2, 3). Tongues were recorded as partially or wholly missing and eye(s) as one or both missing.

The second approach was to calculate minimal-maximal estimtes of overall percentage utilization by predators or scavengers of calf carcasses by category of death as follows. (1) The annual mean viable whole body weight (minimal estimate of utilization) and the annual mean viable whole body weight plus two standard errors of the mean (maximal estimate of utilization) were multiplied by the number of calf carcasses that were in the category. (2) The total weight of carcass remains for all the calves in the category were then subtracted from the resultant values in (1). (3) Then, the two resultant values from (2) were divided by the respective values from (1) and each multiplied by 100.

e.g.

$$\text{Overall \% utilization} = \frac{a(x) - c}{a(x)} \quad \text{to} \quad \frac{b(x) - c}{b(x)}$$

Where:

a = annual mean viable whole body weight;
b = annual mean viable whole body weight plus two standard errors of the mean;
c = total weight of carcass remains in the category; and
x = number of carcasses in the category.

The third approach was to calculate percentage estimations of utilization of individual carcasses of calves <7 d old at death on a weight basis as follows. Percentage utilization equals average whole body weight (based on annual samples) minus carcass weight (for calves with more than 0.25 kg of muscle tissue or viscera missing) divided by the annual average whole weight; all times 100. We choose five utilization classes to group individuals by cause of death: (based on the above calculations) (1) 1-9%; (2) 10-34%; (3) 35-49%; (4) 50-69%; and (5) 70-90%. We then classified carcasses descriptively as (1) minimally used, 1-9%; (2) lightly used, 10-34%; (3) moderately used, 35-49%; and (4) heavily used, 50% or more (50-69% and 70-90%). All carcasses with only eye(s) or tongues were placed in the 1-9% utilization class regardless of carcass weight. Also, any calf whose carcass weight exceeded the mean annual whole body weight was placed in the 1-9% utilization class - regardless of actual degree of utilization.

2.4 Definitions

We developed a glossary of definitions for many words or terms, mostly biological, used in this report to assist the non-technically trained but interested reader (App. 4). We also produced illustrations to help those persons to further understand many of the words and terms defined in the glossary (Figs. 8-10).

2.5 Statistics

Pearson two-way or one-way Chi-square tests and standard F-tests were used where applicable (Mendenhall and Scheaffer 1973, Sokal and Rohlf 1981).

3. Beverly Caribou Herd

The Beverly herd of migratory barren-ground caribou calves on tundra ranges in the west-central District of Keewatin, NWT and calving usually peaks between 4-10 June (Fleck and Gunn 1982; Fig. 1). Postcalving summer ranges are found in both the District of Keewatin and the District of MacKenzie, NWT; winter ranges occur for the most part in the southern District of McKenzie and some years into northern Saskatchewan (Fleck and Gunn 1982; Fig. 1). A detailed annotated bibliography of all aspects of the biology of the Beverly herd (and the adjacent Kaminuriak herd) has been compiled by Williams *et al.* (1983).

The breeding cows and their juvenile followers arrived on an essentially snow covered calving ground by the third week of May in each year of this study (Clements 1982, 1983, Bradley and Gates 1984). Most calving took place during the first 2 weeks of June in all 3 years of this study. In 1981, calving peaked earlier (2-5 June) on the eastern section of the calving ground compared to 7-9 June on the southwest section of the calving ground (Jingfors *et al.* 1982). Again in 1982, calving peaked earlier (9-10 June) on the central portion of the calving ground (high density stratum, Stephenson *et al.* 1983) compared to 11-12 June on the eastern section of the calving ground (medium density stratum) (Gunn *et al.* 1983). In 1983 only one general high (peak) period of calving was discerned, 8-14 June.

The calving ground was of similar size and was located in just about the same area each year from 1981 to 1983 (Fig. 2). However, the relative densities of breeding females appeared to vary somewhat in each year. In 1981 the highest density occurred on the northeastern portion of the calving ground - around Deep Rose Lake; the medium density; and the lowest density occurred further to the west toward Sand Lake. In 1982, the high density and the medium density areas of 1981 were reversed and the medium density area was around Deep Rose Lake while the low density area remained about the same (Stephenson *et al.* 1983). In 1983 the relative densities remained distributed about as in 1982 but the high density area appeared to come further south to the north end of Sand Lake. The general impression was that the main core (highest density) of breeding cows moved progressively southwest from the Deep Rose Lake area in 1981 to the north end and northeast side of Sand Lake in 1983.

In June 1982 the NWT Wildlife Management Division (NWTWMD) carried out a visual aerial survey of caribou on the Beverly calving ground (Stephenson *et al.* 1983). They estimated that breeding cows on the calving ground totalled 42 858 ± 4474. However, the NWTWMD also carried out aerial photography subsampling of caribou on the Beverly calving ground in June 1982 (NWTWMD, unpubl. data) that greatly increased the herd size estimate beyond that which would have been obtained from extrapolation of the visual calving ground estimate. Application of the correction factor based on the difference between number of animals photographed and those visually counted or estimated on a given unit of area gave herd size estimates of 150 000 to 240 000 (or about 195 000 ± 54 000; NWTWMD, unpubl. data). When we assume that about 60% of the herd are females 1-year of age or older and about 70% of them are breeders, we estimate that between 63 000 and 101 000 calves were produced in 1982. We can further assume that this range of calf production would be applicable in 1981 and 1983, as well as in 1982.

RESULTS

The results of this 3-year study are presented on an annual basis to maximize the detail of the findings. Case histories for calves and cows are treated separately for each year under each of the 10 established categories of death that were documented in those years [(1) wolf predation, (2) suspect wolf predation, (3) grizzly bear predation, (4) fetal atelectasis, (5) neonatal atelectasis, (6) suspect fetal or neonatal atelectasis, (7) separation of abandonment (malnutrition/starvation complex), (8) patho-physiological, (9) pneumonia, and (10) unknowns]. We first report on a yearly basis under the above 10 categories the cause of mortality; then carcass utilization by predators or scavengers; and lastly, the occurrence of predators and scavengers on the calving ground.

1. Case Histories - 1981

1.1 Cause of calf mortality

1.1.1 Wolf predation

In May-June 1981 we determined that wolves had killed 23 calves in the sample of 79 dead calves (Tables 3-5). Twenty (87.0%) of the 23 wolf-killed calves had their skulls crushed, fractured, or punctured; two (8.7%) were headless; and one (4.3%) had no wounds to the head. The two headless calves along with a third wolf-killed calf were all found within about 45 m of each other. Two observers had watched a wolf actually kill the third calf whose head was unwounded (bites were restricted to the body). The calf had tooth perforations in the upper rib cage-spine area; the tissues of the right rib cage and right femoral area were severely traumatized; and tooth perforations to the posterior tip of the right diaphragmatic lobe of the lungs had caused profuse hemorrhaging in the thoracic cavity.

1.1.1.1 Sex composition

In May-June 1981 8 (34.8%) of the wolf-killed calves were males, 4 (17.4%) were females, and 11 (47.8%) were of undeterminable sex. However, if the sexes of the calves of unknown sex follow the ratio for the calves of known sex (1 female:2 males) or an expected 50:50 sex ratio, there is no difference between the proportions of wolf-killed calves by sex ($\chi^2 = 2.50$, 1df, $P > 0.10$ or $\chi^2 = 0.66$, 1df, $P > 0.70$). The suggestion tht wolf-killed calves were not selected for by sex in 1981 is, however, limited by the small sample size.

1.1.1.2 Age composition

In May-June 1981 we estimated that all of the 23 wolf-killed calves were 1-week or less of age at death. The proportions of younger (<4 d, 47.8%) and older (4-7+ d, 52.2%) calves did not differ ($\chi^2 = 0.04$, 1df, $P > 0.80$) which suggested no selection by wolves in the killing of the 11 younger (<4 d) against the 12 older (4-7+ d) calves.

We found the first two wolf-killed calves on 31 May and the third one on 3 June 1981. As the 3 calves were estimated to be 4-7 d old at death they were born during the last week of May, which is relatively early for caribou of the Beverly herd. We then found the next six wolf-killed calves between 7 and 8 June: three were estimated as <4 d old (two, <1 d; and one, 1-3 d) at death; and three, 4-7 d old. Between 14 and 20 June we found the remaining 14 wolf-killed calves: eight were <4 d old (three, <1 d; and five, 1-3 d) at death; and six, 4-7 d old.

In 1981 only 9 (39.1%) of the 23 carcasses from wolf-killed calves had lungs present, and those lungs appeared normal. The 14 (60.9%) carcasses without lungs had no signs of physiological or pathological conditions that would have predisposed those calves to death by predation. Therefore, there was no evidence in 1981 for wolf predation being compensatory.

In 1981 the locations of the wolf-killed calves that we found (assuming that we did not miss adjacent kills around single finds) suggested that 43.5% (10) were in clumped associations (Table 6). One clump of three calves was within about 6 to 45 m of each other and the other clump of three was within about 60 to 170 m of each other. The two individuals in each of the two clumped pairs were about 10 and 30 m apart.

1.1.2 Suspect wolf predation

In June 1981 we found the carcasses of 14 calves that we believe were killed by wolves (Tables 4, 5). All carcasses were found as singles (Table 6). Five of the carcasses were males (one, <1 d; two, 4-7 d; and two, 7+ d); five were from calves of undeterminable sex (three, <1 d; and two, 1-3 d); and four were from females (one, <1; one, 1-3 d; one, 4-7 d; and one, 7+ d). Twelve (85.7%) of the carcasses had been utilized: nine had been fed on apparently by both wolves and gulls, and three appeared to have been fed on only by gulls.

None of those 14 carcasses found in June 1981 had fatal head wounds or detectable fatal wounds to major organs. However, 11 (78.6%) exhibited evidence of pre-death trauma. Such evidence included (1) frank blood, blood clots, or hemorrhages in the trachea, larynx, or eye socket; (2) small hemorrhages or contusions on the skull; (3) blood around nose, mouth, or anal tract; (4) congestion of blood in the mesenteric blood vessels; and (5) traumatized areas on limbs and flanks. The other three carcasses had the general appearance of wolf kills: one was found scattered on lake ice about 150 m from shore, one was found sprawled among boulders, and one was found sprawled in a rocky area of a sedge meadow. All three carcasses were heavily utilized, apparently by both wolves and gulls.

1.1.3 Grizzly bear predation

In June 1981 we found one intact carcass of a female, <1 d old, calf (Tables 3-6). The decomposed carcass lay alongside the maternal cow's carcass; both were covered with dirt by the bear. We did not weigh the calf's carcass because its wet and decomposed condition would have distorted the live body weight. The calf had not been cleaned or, at least, not completely cleaned by her mother.

Also in June 1981, ground observers found several single disarticulated limbs from newborn calves of the year scattered on the tundra. More extensive ground searches in some of those areas yielded additional limbs but no torsos or heads. The disarticulated limbs probably were the remains of grizzly bear kills or grizzly bear scavenging activities.

1.1.4 Fetal atelectasis

We found the carcasses of five stillborn calves (four males and one female) that we classified as fetal atelectasis in June 1981 (Tables 3-5). The lungs of all five calves had totally failed to convert from fetal tissue to functional neonatal lungs. All five calves had been only partially cleaned by their mothers: placental remnants were adhering to the pelages; and there were patches of sticky or dried amniotic fluids on the pelages. The total lack of any wear and the soft cartilaginous tips of the hooves indicated that none of the calves had ever walked.

The whole body weights of two males (6.75 and 4.0 kg) and a partial body weight of one other male (5.0 kg) indicated that they had obtained viable body weights. The partial weight of the fourth male calf was not taken. The partial body weight of the one female calf (4.0 kg) suggested that she had also obtained a viable level.

One male calf was found with his mother still standing over him. Another male calf probably had been trodden on by its mother to induce movement or a response. There was a traumatized area on the posterior portion of the skull, but apparently not predator inflicted (no tooth punctures).

1.1.5 Neonatal atelectasis

We determined that 11 calves (seven females and four males) had died of neonatal atelectasis in June 1981 (Tables 3-5). The lungs of all 11 calves had partially failed to convert from fetal tissue to functional neonatal lungs. All but one had been completely cleaned by their mothers. The one exception, a <1 d old male, was only partially cleaned and had never nursed. Nine of the 11 carcasses still had stomachs intact: three of the calves never nursed; four had only a little vegetation in them; and two had milk curds present. (Seven calves showed no wear on their hooves.) The three 1-3 d old females calves and one <1 d old female calf all showed slight wear on their hooves.

Whole body weights for two of them were nonviable (2.5 and 3.0 kg). Partial body weights (3.5 and 4.0 kg) for the other two were light but their whole body weights would have been within the range of viable weights. The other three females were 1-3 d old at death. A whole body weight (4.5 kg) for one and a partial body weight (4.5 kg) for the second one indicated they had obtained viable weights. No weight was recorded for the third one. The whole body weight of one <1 d old male calf was nonviable (2.25 kg); while those of one <1 d old male calf (6.5 kg) and two <1 d old male calves (5.0 and 6.75 kg) were all viable.

A <1 d old female calf was found with the mother standing over the carcass. The cow had cleaned the calf but the calf had never nursed. There had been no conversion of the fetal right diaphragmatic lobe of the lungs; the left diaphragmatic lobe was about 70% converted to neonatal lung; and the apical lobe was fully converted. A second <1 d old female calf was found alive with its mother. The calf was lying on its sternum and it had resorted to open mouth breathing. The cow had cleaned the calf but the calf had never nursed. There was incomplete conversion of all lobes of the lungs from fetal to neonatal tissue. The cow remained in the area while we examined the calf. A third <1 d old female calf was found with incomplete conversion of fetal tissue to neonatal lungs. She also had hemorrhaged areas in the trachea, possibly from her mother stepping on her, if she did not respond to the cleaning process. The fourth <1 d old female calf was found with the majority of the lung tissue still fetal, only the apical lobe was functional. The cow had cleaned the calf but the calf had never nursed.

A 1-3 d old female calf with incomplete conversion of fetal to neonatal lungs may also had been separated from its mother. The calf's anal area was caked with feces. The stomach contained fragments of vegetation and caribou winter hair but no milk. The trace of blood tinged fat on the kidneys suggested poor nutrition. A second 1-3 d old female calf had only about 75% of the left diaphragmatic lobe of the lungs converted from fetal tissue to neonatal lungs and the remainder still in a fetal state. The third 1-3 d old female calf apparently still had its mother nearby, trotting about in the area of the carcass. Only about 50% of the lung tissue had converted from fetal to neonatal lungs. The calf's stomach was full of milk curds.

A <1 d old male calf was found with only minor conversion of the fetal lung tissue to neonatal lungs. The afterbirth had only been partially removed from the calf's pelage and the calf had never nursed.

A <1 d old male calf was found with no conversion of the left diaphagmatic lobe from fetal to neonatal lungs. The cow had cleaned the calf but the calf had never nursed. The calf had apparently been trodden on shortly after birth, probably by the cow to induce movement. There was a skin laceration in the upper quadrant of the right rib cage between the 11th and 12th ribs. Internally there was a laceration of the right lobe of the liver, resulting in a profuse hemorrhage. There was also a hemorrhagic area present on the right diaphragmatic lobe of the lungs. A second <1 d old male calf was found with about 50% of the left diaphragmatic lobe of the lungs still in a fetal state. The cow was standing over the calf when found. She had cleaned the calf but the calf had never nursed. A large number of fecal pellets around the calf's carcass suggested that the cow might have had a difficult time in delivering the calf. The third <1 d old male calf with incomplete lung conversion from fetal to neonatal had some milk curds in its stomach. The protrusion of meconium from the anus suggested that the calf had not nursed much. The calf had possibly been kicked against a rock. There was a skin laceration about 41 mm long, involving the upper left area of the withers and associated with extensive trauma to the subcutaneous tissues of the left shoulder region. There was also a smaller traumatized area involving the right scapula.

1.1.6 Suspect fetal or neonatal atelectasis

We could not fully determine the causes of death for the partial carcasses of eight calves (all <1 d old; one male, two females, and five unknowns) found in June 1981 (Tables 4, 5). The lungs were entirely missing from five of the six carcasses. The sixth carcass had fragments of lung tissue remaining, that was fetal in appearance but it did not sink completely when placed in water.

We classified suspect cases fetal or neonatal atelectasis from placental remnants; dried patches on the pelages apparently of amniotic fluid; hooves that indicated the calves never walked; the absence of predator inflicted injuries or other trauma (except in one case); and the general appearance of the carcasses. One carcass had placental tissue adhering to the entire right side which was the ground side. This calf had hemorrhaged areas on subcutaneous tissues of the right flank and in the trachea. The hemorrhagic condition suggested that the calf was either accidently trodden on by its mother or deliberately stepped on or kicked by its mother to induce movement or response.

1.1.7 Separation or abandonment (malnutrition/starvation complex)

We assigned three calves to this category in June 1981. Only one of the carcasses was still intact (Tables 3-5). All three calves were 4-7 d old females; they were found dead with no milk in their stomachs. No cause of death other than apparent malnutrition/starvation complex could be discerned.

There was still a cow in the general area of the intact calf (5.75 kg) though not close by. The calf only had a few lichens and a small amount of gray pastey substance in its stomach. We guessed that the cow, if it was the calf's mother, probably had mastitis (by the relatively large size of her udder) and because of the pain of infection would not let the calf nurse. Therefore, we considered the calf abandoned by its maternal cow.

1.1.8 Patho-physiological

We found three calves that died from patho-physiological conditions in June 1981 (Table 3-5). Only one of the carcasses was intact.

Two of those three calves apparently died from either accidental or deliberate kicks by their maternal cows or other caribou. One of them, a 1-3 d old female (5.0 kg) was kicked in the right rib cage, causing compression of the thoracic cavity and hemorrhaging in the lungs. Hemorrhages in the mouth were traced from blood clots accumulated throughout the trachea. No broken ribs or evidence of predator inflicted wounds were found. The second of these two calves, a <1 d old of undiscernible sex appeared to have been kicked at the base of the skull, but the carcass had been extensively scavenged.

The third calf, a 4-7 d old male, had died from shock brought on by cold and exhaustion when it fell into near freezing water and could not climb the high surrounding ice shelf. There was no excessive fluid in the trachea and no water could be expressed from the lungs; thus, indicating the calf had not drowned.

1.1.9 Pneumonia

We found two calves that had died of pneumonia in June 1981 (Tables 3-5). One calf a 7+ d old female, had dark circumscribed areas of consolidation in the right diaphragmatic lobe of the lungs: the hepatic appearance was typical of pneumonia. Our assignment of cause of death for the other calf, a 4-7 d old female, was more speculative as no lungs were present. However, we classified this case as pneumonia because the trachea contained foamy fluid - a pneumonic condition; and there was no sign of predator inflicted injury or other trauma.

1.1.10 Unknowns

We found the carcasses of nine calves in June 1981 for which we could not determine the causes of death. All carcasses were too decomposed or too fragmentary for detailed examination. These carcasses classified as unknowns were not used in evaluating the relative frequencies of causes of death to newborn calves but they were used in evaluating the extent of predator utilization or scavenging.

1.2 Causes of cow mortality

In 1981 we found and necropsied seven female caribou. The dead cows ranged in age from 2 to 10+ years.

1.2.1 Wolf predation

In 1981 we found only one cow, a 6-7 yr old that had been killed by a wolf. She had wounds in the cervical area, left flank, and her ribs were removed. The marrow of her femur was firm and waxy to the touch but there was a bloody tinge to its whitish appearance. She had calved but there was no live calf in the area. A carcass of a calf that apparently had been stillborn was found about 100 m away. Several gulls were feeding on the cow when we landed, and a single wolf was seen leaving the area as the helicopter approached.

1.2.2 Grizzly bear predation

In 1981 two cows had been killed by grizzly bears. One cow, a 4-5 yr old, still carried a 7 kg male fetus. The cow had a tooth perforation between the muzzle and eyes which shattered the adjacent turbinate bones and severed the upper jaw, also the anterior right cervical area was extensively traumatized. The marrow of her femur was firm and waxy to the touch and whitish in appearance. Both the cow and her fetus were too decomposed to allow more detailed examinations. The bear had eaten most of one hindquarter, the cheek meat, the tongue, and all viscera. There were over 15 gulls near the carcass when found.

The other cow, a 6-7 yr old, and her <1 d old neonate had been killed by a grizzly bear and covered by the bear with soil and litter. Both carcasses were too imcomplete for detailed information. The grizzly bear had to be driven from the carcasses with the helicopter. The bear made two charges at the helicopter before leaving the area at a strong gallop. There was one gull near the carcasses but was not feeding on them when found.

1.2.3 Birth complications and associated diseases

Four of the seven cows had died from complications associated with giving birth. Two cows had been bred as yearlings and both their fetuses had been partially delivered. Both appeared to have died from exhaustion associated with not being able to successfully pass the fetus through the pelvic cavity.

The first of those 2-yr-old cows with a partially delivered fetus had been dead for some time when found. She had one front foot of her full term fetus protruding some 20 cm from her vulva. Her uterus had contracted around the fetus in a normal position for delivery. The head of the fetus was in the pelvic cavity - the other front foot was not extended through the vagina. The skin of the fetus was dried up; all placental fluids had been expelled; and the fetus was undergoing autolysis, only skin and bones remained. The cow's placental tissues were undergoing putrefaction and the uterine tissues were thickened - indicative of metritis. There had been no rupture of the uterus but there was extensive peritonitis in the abdominal cavity. Most of the abdominal organs and viscera were covered with fibrin tags. We suspect that the peritonitis was an extension from the putrefactive processes involving the uterus. The marrow in her femur was firm and waxy to the touch and whitish in appearance but she completely lacked back fat. The cow appeared to have experienced dystocial conditions during the birth process. She had dried blood present around her nostrils and eye sockets, probably resulting from gull activities when the cow was comatose. Gulls had scavenged the carcass through the rib cage and there were six gulls at the carcass when found.

The second of the 2-yr-old cows with a partially delivered fetus also had been dead for some time when found. She was lying in a pond with her full term fetus partially delivered. The head, front legs, shoulders, and rib cage of her fetus had been delivered and those parts had decayed away to a skeleton. The marrow in her femur was firm and waxy to the touch and whitish in appearance. Her uterus was thickened but the carcass was too decomposed for further examination. There were no gulls present in the area when the carcass was found.

The third cow, a 5-6 yr old, that had died from birth complications had pyelonephritis associated with probably prolapse of her uterus following parturition. The cow had a bloody discharge around her vulval area and her fecal pellets also were bloody. There was no fetus or uterus in the carcass. The left kidney had a multiple foci of absesses (pyelonephritis); there was a marked atrophy of intercostal muscles; and the carcass had an emaciated appearance to it. The marrow of her femur was gelatinous and reddish in appearance. The cow had delivered her calf but then suffered a prolapse of the uterus and an ascending infection of the urethra localized in the left kidney, resulting in multiple absesses. Scavengers had removed the uterus and viscera through the vulval-anal area. Several gulls were present at the carcass when found.

The fourth cow, a 10+ yr old, that had died from birth complications was found with her fetus still retained. No reason could be determined from the postmortem findings for the failure of the cow to deliver her fetus. Bacteriological material was sent to the Manitoba Veterinary Laboratory for examination: no brucella were isolated; a gram smear of pus revealed large gram positive bacilli throughout the slide - possibly bacillus or clostridial organisms. The cow had a bald patch of skin on her lower left cervical area with some trauma to the tissues in that area. There was a bloody vaginal discharge; the cervix was not dialated; the feces were of fluid consistency - probably associated with straining and labour contractions. She had some apparently self-inflicted trauma in the groin area; and there appeared to be some suppuration associated with the cotelydon attachments to the placenta. The marrow of here femur was firm and waxy to the touch and whitish in appearance; but she lacked any back fat; however, she had both mesenteric fat and kidney fat present. The fetus was normal in appearance, except that there were hemorrhagic areas on the fetal lungs. There were no gulls present at the site of the carcass when found.

2. Carcass Use by Predators and/or Scavengers - 1981

We used whole body weights to estimate percentage utilization of carcasses. In May-June 1981 we obtained essentially whole body weights from 17 calves, all 1-week or less of age at death (App. 7). Three of those 17 calves had <0.10 kg of tissue removed: one with its nose severed; and one with its lower jaw missing. However, three carcasses weighed less than 4.0 kg (2.25, 2.50, and 3.00 kg) our arbitrary minimal threshold weight for viable calves. Therefore, we used only the weights from the remaining 14 carcasses to calculate average viable whole body weights in June 1981 (Table 7). We also found an intact carcass of a 7+-d-old male calf that weighed 10.0 kg.

In 1981 79.7% (63) of the 79 calves had been fed on by wolves or gulls (Tables 8-12). Of the 63 carcasses fed on by predators or scavengers 60 were from calves that were 1-week or less of age at death. The total weight using the mean and the mean plus two standard errors (Table 7: 5.70 and 6.38 kg) of those 60 carcasses should have been about 342-383 kg but the measured total weight for them was 169.75 kg. Therefore, total estimated overall utilization of those 60 carcasses amounted to 50-56% (342 - 169.75/342 and 383 - 169.75/383).

In 1981 the rate of utilization among carcasses varied considerably (Tables 8-12). Most carcasses (60.0%) that were fed on received greater than 50% utilization on a percentage utilization class basis (Table 9).

In 1981, 93.6% (59) of the 63 carcasses fed on by predators or scavengers had visceral parts missing; 40 (67.8%) of those 59 had all the viscera taken; and 11 (18.6%) had most and eight (13.6%) only some of the viscera gone (Tables 8-12). Four (21.0%) of the 19 carcasses with some visceral parts remaining had the stomachs and contents present: two of the stomachs were full of milk curds. Both of those carcasses had been scavenged by gulls but neither had been fed on by wolves. Entries to their body cavities were through scavenger-made holes too small for wolves to have fed from. One of the remaining two carcasses with stomachs present had only vegetation in the stomach and the remaining carcass had an empty stomach (never nursed or fed on vegetation). Lungs and liver (whole or partial) were the organs most frequently left in the carcasses in 1981.

In 1981, 68.2% (43) of the 63 carcasses fed on by predators or scavengers had deep muscle tissue missing (Table 11). Removal of muscle tissue from the scapulae and from around femoral bones was most common. Forty-one (96.3%) also had all (80.5%), most (9.8%), or just some (9.7%) of their viscera removed. Heavier utilization resulted in removal of muscle tissue from along the vertebral column and the rump.

In 1981 whole and partial body weights were obtained from 21 of the 23 wolf-killed and 11 suspect wolf-killed calves estimated to be <1-week-old. The other 13 carcasses were more heavily utilized and the weights of the fragmentary remains were not recorded. For the purpose of this exercise, however, we assigned 1.5 kg as the probable average weight for those remains. Thus, the estimated total weight of the 34 carcasses was 107.75 kg. The average overall weight of those 34 calves was 194 kg (5.70 x 34) and the average plus two standard errors (SE = 0.34) overall weight was 217 kg (6.38 x 34). Therefore the estimate of average overall utilization was 44.4 to 50.3% (194 - 107.75/194 and 217 - 107.75/217).

In 1981, 31 of the 32 calves that died of non-predator causes were estimated to be <1-week-old. Based on the above procedure using a total weight of 118.5 kg for the remains of the 31 carcasses we estimated average overall utilization at 33.0 to 40.2% ((5.70 x 31) - 118.5/177 and (6.38 x 31) - 118.5/198). In 1981 carcasses of six of the nine calves that died of undiscerned causes were only fragmentary remains. Therefore, the above procedure using a total weight of 15.75 kg for the nine carcasses gives a relatively high average overall estimate of utilization at 69.1 to 72.4% ((5.70 x 9) - 16/51) and (6.38 x 9) - 16/57).

2.1 Wolf predation

In 1981, 82.6% (19) of the 23 calves killed by wolves were fed on apparently by both wolves and gulls and one of the 23 calves was scavenged only by gulls which had pecked away some tissue around the anus. The remaining three carcasses were unutilized.

Only three of the 20 carcasses had not had muscle tissue taken but all, most, or some of their viscera had been removed (Table 10). Most (88.2%, 15/17) of the 17 carcasses which had muscle tissue removed also had all the viscera removed (Table 11). The percentage utilization of the carcasses is calculated for all 20 carcasses as they were <7 d of age at death (Table 12). Twelve (60.0%) of those 20 carcasses were heavily utilized and only four were lightly or minimally utilized.

2.2 Suspect wolf predation

In 1981, 64.3% (9) of the 14 calves suspected of having been killed by wolves were fed on by both wolves and gulls. Four carcasses had been fed on to a small extent by gulls only and one carcass was untouched.

Most of the seven calves (71.4%, 5/7) with intact muscle tissue had all or most of the viscera removed (Table 10), and the other six calves who had muscle tissue taken, had also lost all of their viscera (Table 11). Percentage carcass utilization could be calculated for only 11 of the 13 carcasses as two were >7 d old at death. Most (63.6%) of those 11 calves were heavily utilized and four were lightly or minimally utilized on a weight basis (Table 12).

2.3 Grizzly bear predation

In June 1981, the single grizzly bear-killed calf had already been utilized by the bear or possibly by scavengers when found. The bear was apparently keeping scavengers out of the cache mound. There was one gull nearby but it was not feeding on the carcass when found.

2.4 Fetal atelectasis

Gulls had scavenged three of the five calves that had died from fetal atelectasis in June 1981. Only one of the carcasses had intact muscle tissue but most of its viscera had been removed (Table 10). Some muscle tissue and some viscera (stomachs only) had been taken from the other two carcasses (Table 11). Use by scavengers was heavy in one case (based on an estimated weight of 1.5 kg) and light in the other two (Table 12).

2.5 Neonatal atelectasis

Gulls had scavenged only four of the 11 calves with neonatal atelectasis in June 1981. One calf had only some of its viscera taken (Table 10). The other three calves had muscle tissue missing; two of them also had lost most or some of their viscera and the third calf had only lost an eye and some tissue around the anus (Table 11). Two of the calves had been heavily or moderately scavenged and the other two only lightly utilized (Table 12).

2.6 Suspect fetal or neonatal atelectasis

Gulls had scavenged all eight calves that were suspected cases of fetal or neonatal atelectasis in June 1981. The two carcasses with no muscle tissue removed had all their viscera removed (Table 10). The viscera were completely removed in four and mostly gone in two of the six carcasses which had muscle tissue removed (Table 11). Most of the eight carcasses which were all aged <7 d at death (62.5%, 5/8) were heavily utilized (Table 12).

The other three calves which had all their viscera gone but less or none of their muscle tissue removed were lightly utilized (Table 12).

2.7 Separation or abandonment (malnutrition/starvation complex)

Gulls had scavenged two of the three calves that had succumbed as a result of separation from their mothers. Neither carcass had muscle tissue removed (Table 10). One carcass had most of it viscera removed (Table 11), although on a weight basis it was classified as only minimally utilized (Table 12). The second carcass was also classified as minimally utilized (Table 12) but no viscera or muscle had been fed on; only an eye had been taken (Table 10).

2.8 Patho-physiological

Gulls had scavenged two of the three calves that had died from patho-physiological causes in June 1981. One calf had some viscera but no muscle removed (Table 10) and the second calf had essentially all its viscera and deep muscle tissue removed (Table 11). The later one was classified as heavily utilized and the former as only lightly utilized (Table 12).

2.9 Pneumonia

Gulls had scavenged both calves that had died from pneumonia in June 1981. Most of the viscera had been removed from the calf with intact muscles (Table 10) and all the viscera from the calf which had lost some muscle tissue (Table 11). The first calf was placed in the lightly utilized class (Table 12). The second calf (8.0 kg) was >7 d at death and its utilization on a weight basis was not calculated.

2.10 Unknowns

The nine calves had been utilized by gulls to the extent that no causes of death were evident. Only two carcasses still had muscle tissue but no viscera (Table 10). All the viscera had been taken in six of the seven calves that had lost muscle tissue and the seventh calf had some viscera removed (Table 11). All of the nine carcasses were ranked as heavily utilized on a weight basis (Table 12).

3. Occurrence of Predators and Scavengers - 1981

3.1 Wolves

In 1981 we saw only 12 wolves on 10 occasions: eight singles; and two pairs. Wolves were seen at the sites of two wolf-killed calves: two wolves on one occasion; and a single wolf on the second occasion. A single wolf was seen killing a third calf, the carcass of which was subsequently retrieved by the ground observers. (This wolf also killed three more calves, not included in our 1981 sample).

3.2 Grizzly bears

In 1981 we saw nine grizzly bears: singles on seven occasions; and a female plus yearling on two occasions. Only one grizzly was seen at a cache mound that contained a grizzly bear-killed cow and her calf.

3.3 Gulls

In 1981 gulls were at 23 (29.1%) of the 79 calf carcasses when found (Table 13). We were able to count exact numbers on 10 (43.5%) occasions: five singles; two groups of three; and one group of four, five, and six each. On the other 13 (56.5%) occasions, some of the gulls were flying away from the carcasses well in advance of our close approach; and on those occasions, numbers of gulls were recorded simply as - several gulls present. On those occasions, numbers of gulls most likely ranged between six to 20 birds; most often, more than 10 at each site. Gulls were at five (71.4%) carcasses of the seven dead cows when found: from one to 15 birds at each site (1, 6+, 6+, 6 and 15).

3.4 Minor scavengers

We saw only one arctic fox in June 1981 and no active fox dens. Rough-legged hawks were relatively common on the calving ground in May-June 1981 but we saw only one rough-legged hawk at each of two carcasses and signs of rough-legged hawks having been at two other carcass sites. On one occasion, we observed a Sabine's gull (*Xema sabini*) feeding on the carcass of a yearling caribou. Long-tailed and parasitic jaegers were seen on several occasions and golden eagles and ravens on even fewer occasions in May-June 1981 (None were seen on or near caribou carcasses).

4. Case Histories - 1982

4.1 Causes of calf mortality

4.1.1 Wolf predation

In June 1982 we determined that wolves had killed 69 calves in the sample of 107 dead calves (Tables 3, 4, 14). Sixty-six (95.6%) of the 69 wolf-killed calves had their skulls crushed, fractured, or punctured; two had their heads missing; and one had no injuries to the head. As in 1981, the two headless calves were found within metres of each other: one had been seized by the throat and the back of the neck, the other showed traumatized areas on the neck and upper portions of both hind legs. The calf with no head wounds had massive traumatized areas on both sides of the rib cage and tooth penetration into the left thoracic area, causing hemorrhaging in the left diaphragmatic lobe of the lungs.

The inclusion of 34 wolf-killed calves found on one occasion within a 3 km^2 area likely causes an over-representation of the percentage of wolf-killed calves (75.0%, n = 92) in 1982. Percentage occurence of wolf-killed calves in the sample of 92 (15 unknowns deleted) for the first 37 calf carcasses found was 70.3% (26). Percentage occurrence of wolf-killed calves among the 39 calf carcasses found on the 3 km^2 area was greater, 87.2% (34). Percentage occurrence of wolf-killed calves for the last 16 calf carcasses collected equaled 68.8% (11). Therefore, the most representative percentage of wolf-killed calves is 69.8% (37) based on the 53 calf carcasses found outside the 3 km^2 area.

4.1.1.1 Sex composition

In June 1982, 32 of the wolf-killed calves were males, 24 were females, and 13 were of undeterminable sex. The proportion of wolf-killed female calves does not differ from the proportion of wolf-killed male calves ($\chi^2 = 1.10$, 1df, $P > 0.30$). Even when we assign the 13 calves of unknown sex to the calves of known sex at the observed sex ratio (three females:four males) or the expected 50:50 sex ratio we do not obtain any significant differences ($P > 0.20$ and $P > 0.30$). The wolves apparently were not selecting calves on the basis of the calf's sex in 1982.

In June 1982, the 34 calves killed and found within 24 hours on only a 3 km^2 land area gave the best analysis of possible selection by sex 14 female, 16 male, and 4 unknown calves. This result further strengthens our assumption that wolves did not select calves by sex or that one sex was more vulnerable than the other sex in June 1982.

4.1.1.2 Age composition

In June 1982 we estimated that 67 of the 69 wolf-killed calves were 1-week or less of age at death and only two calves were aged 1-2 weeks old. The proportion of young (<4 d, 79.7%) calves differed from the proportion of older 4-7+ d, 20.3%) calves killed by wolves ($\chi^2 = 24.02$, 1df, P <0.001) which suggests wolves selected younger (<4 d) rather than older (4-7+ d) calves.

Only eight (11.6%) wolf-killed calves were found (one, 8 June; six, 9 June; and one, 13 June) during the period of greatest calving in 1982: all were estimated to be <4 d old at death. The remaining 61 wolf-killed calves were found between 14 and 18 June during the early postcalving period in 1982. Of those calves, 47 (77.0%) were estimated to be <4 d old at death and 14 (23.0%) were 4-7+ d old. The occurrence of 3.4 <4 d old calves among the wolf-killed calves after the peak of calving to every one 4-7+ d old calf argues strongly for wolves selecting younger calves in mid June 1982. A one-way Chi-square test of the 47 calves (<4 d) against the 14 calves (4-7+ d), based on equal representation at 30.5 calves, gives a significant difference (χ^2 17.78, 1 df, P <0.001). This further allows us to accept that, in June 1982, wolves took proportionately more younger (<4 d) calves than they did older (4-7+ d) calves. Also, either more calving took place after 12 June 1982 or late born calves were especially vulnerable to wolf predation.

In 1982, 25 (36.2%) of the 69 carcasses from wolf-killed calves had lung tissue present. The lungs from two (8.0%) of those 25 calves revealed that the calves had neonatal atelectasis, and their deaths by wolves could be considered compensatory. The 44 (63.8%) carcasses with no lung tissues remaining showed no evidence of any physiological or pathological conditions that would have made them vulnerable to wolf predation.

In 1982 the locations of the wolf-killed calves that we found (assuming that we did not miss adjacent kills) suggested that 75.4% (52) were in clumped associations (Table 15).
The two individual calves in each of the two pairs were within about 100 m of each other. The 11 wolf-killed calves found together in 1982 were on a small island only several hundred square metres in size in a large lake (Deep Rose Lake). A pack of five white wolves, the largest pack of wolves seen on the calving ground during the three calving and postcalving periods (1981-83) had been seen on the island by two ground observers a few days before some of the carcasses were collected by the ground observers and some more were found by a subsequent aerial search of the island.

On 17 June 1982 during helicopter searches we found 34 carcasses from wolf-killed calves within a 3 km^2 area, centered at 65°46'N, 99°17'W. All of the calves had been killed by wolves, all within a short period of time of each other and all within about the last 24 h. All 34 carcasses had crushed, fractured, and tooth punctured skulls, and considerable traumatized areas over their bodies. Hemorrhaging associated with wounds indicated the wounds were inflicted while the calves were alive.

Seventeen of the 34 carcasses of the wolf-killed calves were on a flat topped, boulder-strewn ridge: the vegetation was predominantly lichens and prostrate ericaceous shrubs. Five antlerless cows were walking and grunting on the ridge, probably searching for their calves. The caribou had galloped down a snow-covered bank (30-40 cm deep) where three calf carcasses were found alongside deeply furrowed trails. Four and three carcasses were found on the ice-covered lake and opposite snow-covered bank, respectively. Above the opposite bank the trails crossed a rugged boulder field where we found seven carcasses.

4.1.2 Suspect wolf predation

In June 1982 we found the carcasses of two calves that we believe were killed by wolves (Tables 4, 14). The two carcasses were found as singles (Table 14). Even though both carcasses had been extensively utilized, apparently by both wolves and gulls, they still exhibited pre-death trauma.

One carcass from a <1 d old calf of undeterminable sex which had minor hemorrhaging on the neck although much of the skin and outer flesh had been removed. The other carcass was a 1-3 d old female calf that had probable signs of trauma on the skull, which had been cleaned up by maggots. The skull was disarticulated from the neck (although possibly the result of maggot feeding).

4.1.3 Grizzly bear predation

In June 1982 we found no grizzly bear-killed calves or disarticulated limbs from calves that implicated predation or scavenging, although we had the same number of ground observers (6) in 1982 as in 1981.

4.1.4 Fetal atelectasis

We found the carcasses of four apparently stillborn male calves that we classified as fetal atelectasis in June 1982 (Tables 3, 4, 14). The lungs of all four calves had totally failed to convert from fetal tissue to functional neonatal lungs. All four had been only partially cleaned by their mothers as there were placental remnants adhering to and patches of sticky amniotic fluids on the calves' pelage. The total lack of any wear and the soft cartilaginous tips of the hooves indicated that none of the calves had ever walked.

The essentially whole body weights of three of them (7.0, 6.5, and 5.5 kg) exceeded the viable threshold body weight. The partial body weight of the fourth one (2.75 kg) suggested that its whole weight had been at least borderline viable (about 4.0 kg).

One male was still being delivered when first seen. The cow was walking with about the posterior half of the fetus hanging out. The cow appeared to be in agony and had difficulty in walking. She finally expelled the fetus from a lying position. The fetus was delivered hind feet first and the amniotic sac was only attached to its head and shoulders. We suspect that the shoulders and head of the fetus lodged at the pelvic brim; when the cow went down, she probably relaxed more and permitted better positioning of the fetus and allowed delivery. When the cow got up she paid no attention to her dead neonate (which had probably died as a fetus). The cow then staggered for several steps, almost falling over with each step. She then began walking stiff-legged for several hundred metres often pausing seemingly to strain, before gaining back her legs and beginning to forage.

4.1.5 Neonatal atelectasis

We found five carcasses of calves (three females and two males) that died of neonatal atelectasis in June 1982 (Tables 3, 4, 14). The lungs of all five calves had partially failed to convert from fetal tissue to functional neonatal lungs. All of them had been completely cleaned by their mothers and they had probably nursed though the four with stomachs had no milk curds (three had a little vegetation and one was essentially empty). The lack of wear on their hooves suggested that although they had walked about they had not travelled much.

The whole body weight of one female was a nonviable 2.75 kg. The essentially whole body weights of the two males (5.75 kg and 5.0 kg) and one of the females (5.25 kg) exceeded the viable threshold body weight. The partial body weight (3.75 kg) of another female suggested that she had also reached a viable level.

The <1 d old female calf (2.75 kg) still had fetal lung tissue in about 90% of the apical lobe, and in about 75% of the right and 10% of the left diaphragmatic lobes of her lungs. An antlered cow, the mother, was standing over the carcass; she trotted away grunting loudly as we landed. The calf's stomach was essentially empty.

The two other females were 1-3 d old: one had only a little vegetation in her stomach and the other carcass had no stomach. A cow was standing over the former and she trotted away vocalizing as we landed. The calf still had fetal lung tissue in about 90% and 5% (around border) of the left and right diaphragmatic lobes of the lungs, respectively. The other calf still had fetal lung tissue in about 80% of the apical lobe, and in about 50% of both the left and right diaphragmatic lobes of the lungs.

The two male calves were 1-3 d old: both had only a little vegetation present in their stomachs. One male still had fetal lung tissue in about 95% of all lobes of his lungs, and the other male had fetal lung tissue in about 50% of both the left and right diaphragmatic lobes and about 40% in the apical lobe of his lungs.

4.1.6 Suspect fetal or neonatal atelectasis

We found no carcasses of calves to which we could not assign the cause(s) of death but showed signs of being possible suspect cases of fetal or neonatal atelectasis in June 1982.

4.1.7 Separation or abandonment (malnutrition/starvation complex)

Two of three calves in this category in June 1982 were found alive (Tables 3, 4, 14). One, a 1-3 d old male (5.0 kg), was seen stumbling and alternately collapsing and bleating in a meadow. He had no milk curds and only a little vegetation in his essentially empty stomach. The other calf, also a 1-3 d old male (8.5 kg), was found curled up in a tussock meadow about 50 m from another calf with a broken leg. His stomach was full of vegetation and some milk, but he was too weak to evade being caught. The third calf, a 1-3 d old male, was found dead with only vegetation in his stomach (and no other apparent cause of death).

4.1.8 Patho-physiological

We found five calves that died from patho-physiological conditions in June 1982 (Tables 3, 4, 14). Three of the five carcasses were intact.

The proximal cause of death for two of those calves was a malnutrition/starvation complex. A third calf would have succumbed to malnutrition/starvation or a predator, if it had not been killed by us. The fourth calf died of an infection. The fifth calf died from an undetermined proximal cause.

A <1-d old male calf (3.75 kg) suffered from an odd articulation of the left foreleg and the hind feet were bent foreward (flexed tendons). The calf also has a mandibular condition known as 'parrot mouth'. He had never nursed, probably because of the combined complications of distorted foreleg, hind feet and shortened mandible. Most likely exhaustion was brought on by failure to feed and the calf succumbed to malnutrition/starvation.

A 1-3 d old male calf succumbed to malnutrition/starvation because his maternal cow died of a ruptured uterus. The calf's stomach was essentially empty - little vegetation. The calf appeared to have been cleaned by his mother but apparently had not been nursed by her. The calf was placed in this category because of the cow's apparent failure to produce milk.

A 7+ d old male calf (9.5 kg) suffered compound fracture of the hind leg; possibly, it was trampled when its group took flight from some perceived danger; its maternal cow returned to the site, and she approached while we examined the calf (a second calf was found about 50 m away, apparently separated from its maternal cow).

A 1-3 d old male calf (6.25 kg) apparently died from peritonitis associated with the infection of its umbilical cord. His liver was covered with fibrin tags and frank pus which was also on the diaphragm. There were adhesions between abomasum and diaphragm and splenic adhesions to the diaphragm. A hemorrhaged area on the posterior ventral portion of the rib cage and a hemorrhaged area on left cervical area might have been caused by the maternal cow attempting to get the calf up. An antlerless cow, with a markedly enlarged udder, apparently the dead calf's mother, was standing nearby.

A <1 d old calf of undeterminable sex had hydrocephalus - abnormal displacement of frontal bones - probably associated with blockage of cerbral spinal fluid through the ventricles. The calf had a short muzzle and a pronounced brow. The calf had nursed and still had milk curds in its stomach. The actual proximal cause of death was undetermined as the carcass was too decomposed to obtain brain tissue for histo-pathological examination.

4.1.9 Pneumonia

Two of the four calves that died of pneumonia in June 1982 (Tables 3, 4, 14) were still intact. The two 1-3 d old male calves (only one intact - 4.75 kg) had mostly pneumonic patches in all lobes of the lungs. A 1-3 d old female calf (6.0 kg) had mostly pneumonic patches throughout the left and right diaphragmatic lobes of the lungs but the entire apical lobe was normal in appearance. A 4-7 d old female calf had pneumonic patches throughout all the lobes of her lungs.

The stomachs of the three 1-3 d old calves contained only vegetation, indicating that they had not been nursing well sometime before their deaths. The 1-3 d old female still had her mother standing over her when found. The 4-7 d old female had milk curds and vegetation in her stomach. An antlerless cow, the mother, was present and was chasing gulls away from the calf's carcass, but when the helicopter was only about 30 m away she trotted away.

4.1.10 Unknowns

We could not determine the causes of death for 15 calves in June 1982 because all the carcasses were too decomposed or too fragmentary to allow detailed examination. Those carcasses were classified as unknowns and are not used in evaluating the relative frequencies of causes of death to newborn calves but they were used in evaluating the extent of predator utilization or scavenging.

4.2 Causes of cow mortality

In 1982 we found nine but necropsied only six dead cows. Two of the carcasses could not be retrieved from waterbodies and the third one was too decomposed to examine. The six cows necropsied ranged in age from 2 to 6-8 yr old.

4.2.1 Wolf predation

In 1982 the one cow, a non-pregnant 2-yr-old, that was a wolf-kill had been dead for some time before being found. The wolf had seized the cow's lower cervical area at the point of entry to the thorax, and the right mandible was shattered. The neck had tooth puncture wounds and hemorrhaged and traumatized areas. The marrow of her femur was soft and bloody but still partly waxy to the touch and pinkish in appearance. She had besnoitiosis on the muscles and tendons of the right foreleg. There was no evidence of predator feeding on the carcass. There were six gulls on the carcass and it had been scavenged through the rib cage, flank, and anal area. The eyes, lungs, heart, liver, stomach, kidneys, and intestinal tract had been removed.

4.2.2 Grizzly bear predation

No evidence was found in 1982 of grizzly bear predation on adult cows on the calving ground during calving or early postcalving periods.

4.2.3 Birth complications and associated diseases

In 1982 four of the six cows found had died from complications or disease associated with giving birth.

One cow, a 4-5 yr old, had died from a ruptured uterus after giving birth to a male neonate. The cow was stretched out on her side with her dead calf curled up between her fore and hind legs. The cow's hindquarters were blood stained and there was blood in the abdominal cavity - possibly from the ruptured uterus. Gulls had fed through the anal area, rib cage, and flank and removed her eyes, liver, stomach, kidneys, and intestinal tract. Three gulls were present when we found the carcasses. The calf had succumbed apparently to malnutrition and starvation due to his mother's death.

A second cow, 5-6 yr old, with birth complications had died from peritonitis probably from a prolapsed uterus after parturition. No calf was with the cow when she was found. The cow had blood in her nostrils and mouth; most of her body organs were covered with fibrin tabs, with some areas of frank yellowish pus. Her lower forelegs were traumatized - possibly self-inflicted during agonal spasms. The marrow fat of her femur was only of medium firmness and moderately waxy to the touch and reddish in appearance. Gulls had scavenged the anterior half of the tongue and the right eye. There were four gulls on the carcass when found.

A third cow, 6-7 yr old, died from dystocia: the fetus had its forelegs out but the head was turned back in the canal, resulting in too large a mass to pass through the pelvic girdle. The marrow of her femur was of medium firmness and moderately waxy to the touch and pinkish in appearance. Gulls had removed the right eye and pecked holes in the flank and shoulder. There were two gulls on the carcass when found.

A fourth cow, 6-7 yr old, apparently died of injuries sustained during calving. The blood in her mouth and generalized trauma along her back to the vaginal area were suggestive of an extremely difficult birth. The vagina was enlarged, the uterus was partially involuted, the cotyledons were small, and the cow probably had metritis - suggesting that it had been 2-3 weeks since she gave birth. The marrow of her femur was firm and waxy to the touch and whitish in appearance. No live calf was seen though a wolf-killed calf was found nearby, but its relationship to the dead cow is unknown. The left eye of the cow had been scavenged by gulls and there were four gulls near the carcass when found.

4.2.4 Unknowns

In 1982 we could not discern the cause of death of a non-pregnant 2-yr-old cow. The cow's carcass exhibited no evidence of predation, no signs of disease, or any physiological problems except possibly malnutrition. The marrow of her femur was firm and waxy to the touch but pinkish in appearance. The carcass had been scavenged by gulls through the abdomen and part of the liver had been taken. Gulls had also removed the anterior half of the tongue and the left eye, and they had pecked holes in the rib cage and neck. There were 20 gulls near the carcass when we landed.

5. Carcass Use by Predators and/or Scavengers - 1982

In June 1982 we obtained whole body weights from 31 calves, all 1-week or less of age at death. We used only the weights from 29 carcasses to calculate an average for viable whole body weights (Table 16) because two carcasses weighed less than 4.0 kg (2.75 and 3.75 kg) our arbitrary minimal threshold weight for viable calves. We also found one whole carcass from a 7+-d-old male calf that weighed 9.5 kg.

In 1982 97.9% (93) of the 95 utilized carcasses were from calves that were 1-week or less of age at death (Tables 8, 9, 17, 18, 20). Twenty of those 93 carcasses had less than 0.25 kg of tissue removed (19 had tongues or eye(s) removed, and one was scavenged through the rib cage though little or no tissue removed). Those 20 carcasses were used as whole body weights in the set of 29. The remaining 73 carcasses should have weighed 445-472 kg (Table 15) but the measured total weight was 167.5 kg. Therefore, total estimated utilization of those 73 calf carcasses amounted to 62-64% (445 - 167.5/445 and 472 - 167.5/472). The rate of utilization among carcasses, however, varied considerably (Tables 8, 9, 17-20) and most carcasses (65.6%) were less than half fed on.

In 1982 90.6% (97) of the 107 calves had been fed on by wolves or gulls (Tables 17-20). In 1982, wolves or scavengers fed on 98.6% (68) of the 69 wolf-killed calves and both of the suspect wolf-kills (Tables 17-20). In 77.1% (54) of the 70 utilized calves body entries had been made apparently by wolves, but only once had one of the 70 carcasses not been subsequently scavenged by gulls. Therefore, the amount of carcass utilization by wolves versus gulls could not be separated. The remaining 16 (22.9%) of the 70 utilized carcasses were scavenged only by gulls as the entry holes into the body cavities were too small for wolves to have used. The utilization of eye(s) and tongues from calves likely was only by gulls. Only the carcass of one wolf-killed calf was uneaten.

Wolves had not fed on any of the 21 calves that died of non-predator causes in 1982. Ten (47.6%) of those 21 carcasses had been scavenged by gulls only and the remaining 11 (52.4%) had not been scavenged. Thirteen of the 15 calves that died of undiscerned causes were too heavily utilized to determine if they were fed on by wolves as well as by gulls. The remaining two of those 15 carcasses had been used by scavengers only - entry was through small scavenger-made holes (one calf in the anal area, and the other calf in the anal area and rib cage).

In 1982, 78.9% (75) of the 95 carcasses fed on by predators or scavengers had visceral parts missing: 56 had all the viscera taken; and 19 had most or only some visceral parts gone (Tables 17-20). Four (21.0%) of the 19 carcasses still had stomachs which were filled with milk curds. Three of those four carcasses were scavenged by gulls only but we could not discern whether wolves as well as gulls fed on the fourth carcass. Lungs (whole or partial) and heart were the organs most frequently left in the carcass in 1982.

In 1982, 49.5% (47) of the 95 carcasses fed on by predators or scavengers had deep muscle tissue removed (Tables 18, 19). All of them also had all (89.4%), most (8.5%) or just some (2.1%) of the viscera removed (Tables 18, 19).

In 1982, 20 of the 21 calves that died of non-predator causes were estimated to be <1-week-old and the mean whole weight of the 14 intact carcasses was 5.75 kg (Table 16). The range of total weight of those 20 calves calculated from the mean weight (5.75 kg) and the mean plus two standard errors (5.75 + 2 (0.29)) was 115 to 127 kg. The total weight of the carcass remains of those 20 calves equaled 102 kg. Therefore, an approximation of the average utilization of those carcasses would be 11% to 20% (115-102/115 and 127-102/127).

When we apply 6.09 kg as the average whole weight of all 29 calves (Table 16) and 6.47 kg as the average weight plus two standard errors to the 15 calves for which no causes of death could be discerned in 1982, we get theoretical total carcass weights of 91 and 97 kg. As total weight of the remains of those 15 carcasses was only 46 kg a measure of utilization of those calves was 50.0% to 53.0% (91-46/91 and 97-46/97).

5.1 Wolf predation

We judged that 73.9% (51) of the 69 carcasses of wolf-killed calves were fed on by wolves and scavenged by gulls, 23.2% (16) carcasses were scavenged by gulls only; an additional carcass (1.4%) was fed on by a wolf only and one (1.4%) carcass was not utilized (Table 21). Utilization of individual carcasses varied from 1-9% to about 90% utilized and overall utilization of carcasses was low (Tables 20, 21).

In 1982 the average whole carcass weight of 15 wolf-killed calves <7 d old that were not fed on or that scavengers only slightly used (eye(s) or anterial portions of tongues only) was calculated as 6.42 kg (Table 16). Then, the average overall weight of the 69 wolf-killed calves (67 wolf kills, two suspect wolf kills estimated to be <1-week old) should be 443 kg (6.42 x 69); and the average overall weight plus two standard errors (SE = 0.23) of those 69 calves would be 475 kg (6.88 x 69). The total weight of the carcass remains of those 69 calves was 300 kg. Therefore, a rough measure of the degree of utilization on an average overall weight basis would be 32% to 37% (443-300/443 and 475-300/475). Although wolves possibly fed on 75.4% (52) of the 69 calves (<1-week-old) that they killed, on average, the wolves only utilized about 33% of each carcass on a weight basis.

5.1.1 Carcass handling and utilization by both wolves and gulls

We determined the points of body entries by wolves or gulls into the thoracic or abdominal cavities of wolf-killed calves for 74.5% (38) of the 51 carcasses that were fed on by wolves and scavenged by gulls (Table 22). The 13 remaining carcasses were too heavily utilized to determine the original points of entry to the body cavities. Thirty-three (86.8%) of the 38 carcasses had thoracic or abdominal entries through the rib cage, 27 (71.0%) had entries through the flank, and only six (15.8%) through the abdomen. Thirty-one of those 33 carcasses had some ribs broken, severed, or separated which suggested that wolves had made those body cavity entries involving the rib cage in all 31 carcasses. In six cases where the ribs were separated but not broken or missing the wolf entries had been at the posterior margin of the rib cage in the area of the free ribs: four entries also involved the flanks; and two were restricted to the rib cage. The two remaining carcasses had intact rib cages: scavenging gulls had entered the thoracic cavity each through a single intercostal hole and the wolf entry was through a hole in the flank. The entries in 67.7% (21) of those 31 carcasses with damaged rib cages were all associated with larger areas of apparent wolf-entry through the flank and/or abdomen. Body entries in those 21 carcasses were through the rib cage and flank 71.4% (15) of the time; through the rib cage, abdomen, and flank 23.8% (5) of the time; and through the rib cage and abdomen 4.8% (1) of the time. One additional rib cage entry by a wolf was associated with a gull entry in the anal area and some scavenging on the left shoulder. The nine remaining wolf entries through the rib cage were restricted to that area.

Forty-five of the 51 calf carcasses utilized by both wolves and gulls had all or part of their tongues removed and 43 had their eye(s) removed by wolves or gulls (Table 22). The tongue was totally removed from 42 carcasses and only partially gone from the other three carcasses. Both eyes were removed from 30 carcasses; only the left eye from another seven carcasses; and only the right eye from the remaining six carcasses. We believe that gulls removed all or part of the tongues on all occasions by entry through the mouth and the eye(s) on all occasions by pecking in the eye sockets.

The heads were partially removed from 10 of the 51 carcasses. The missing portion of the head was restricted to the cranial vault in nine cases and in one case the nasal and turbinate bones of the face. Eight of those 10 heads had the tongues and eyes missing but the tongues and eyes were still present in the other two heads. In all eight cases gulls, and not wolves, had apparently removed the tongues and eyes.

In 15.7% (8 cases) gulls had pecked holes in the anal area to gain entry to the abdominal cavity (Table 20). We never saw any evidence to suggest that wolves had gained entry to the abdominal cavity by tearing out muscle tissue in the anal area.

Overall utilization was greatest on the 49 carcasses of wolf-killed calves <7 d old (two of the 51 calves were 7+ d old at death) apparently fed on by wolves and scavenged by gulls: 39 to 43%, (298 - 181.25/298 and 317 - 181.25/317). The complete viscera were taken along with most (n = 22), some (n = 8), or none (n = 11) of the deep muscle masses from 41 of the 51 carcasses (Table 17). The other 10 carcasses had most of the viscera removed along with some (n = 4) or none (n = 6) of the deep muscle masses (Table 18).

5.1.2 Carcass handling and utilization only by gulls

Only 37.5% (6) of the 16 carcasses had body entries in them (Table 22): all were single, scavenger-made holes. Three entries were gained through the rib cage; two through the flank; and one in the anal area. No subsequent feeding could be discerned in two of the entries through the rib cage and both entries through the flank. One 1-3 d old female calf (5.5 kg) had only part of the stomach and some of the intestinal tract removed through the rib cage. A second 1-3 d old female calf (5.5 kg) had only some of the intestinal tract removed through the anal area. The remaining 10 carcasses had no entries into their body cavities but their tongue or eye(s) had been removed: seven, the tongue and eye(s); two tongue only; and one, eye(s) only.

The tongue was taken from 75.0% of the 16 carcasses (Table 19), totally removed in eight cases and partially removed in four cases. The eye(s) were taken from 81.2% of the 16 carcasses (Table 19): both eyes in three cases, the right eye in another seven cases and the left eye in the remaining three cases.

The light overall utilization of these 16 carcasses of wolf-killed calves that were only scavenged by gulls limits the evaluation of use on a weight basis. The 16 carcasses totalled 99.5 kg and the average total weight for whole carcasses in only 97.4 kg (6.09 x 16), thus the calculated measure of utilization was negative (-2.6%) and inapplicable. The maximum measure of utilization, based on the mean plus two standard errors (6.47 kg), suggests that all 16 carcasses received only about 4.3% utilization (104 - 99.5/104). The degree of individual carcass utilization was markedly lower for these 16 wolf-killed carcasses (1-9% to only 10-34%) compared to the 49 wolf kills fed on by wolves and gulls (Table 21).

There were two marked differences between the pattern for points of entry into the body cavities of carcasses of wolf-killed calves scavenged only by gulls with the pattern of carcasses of wolf-killed calves fed on apparently by wolves and scavenged by gulls.

(1) There were no abdominal entries by gulls only.
(2) There were no single entries by gulls involving more than one site in combination. That is, all carcasses that were scavenged by only gulls with entries in both the rib cage and flank had separate holes in those areas rather than one continuous hole in carcasses that apparently were both fed on by wolves and scavenged by gulls.

5.1.3 Carcass handling and utilization only by a wolf

The carcass of a 4-7 d old female wolf-killed calf that apparently was fed on by a wolf only, but not scavenged by gulls, was

10 to 15% utilized (6.09 - 5.5/6.09 and 6.47 - 5.5/6.47). On an individual carcass basis the level of utilization fell in the 10-34% class (Table 22).

5.1.4 Carcass handling and utilization of the 34 wolf-killed calves on a 3-km^2 area

Wolves had not fed on 17 of the 34 wolf-killed calves but only one of those carcasses was intact, the remaining 16 carcasses had been slightly scavenged by gulls. One carcass had only an intercostal hole with no parts missing but the other carcasses had portions missing: 12.5% (2) one eye; 6.3% (1) both eyes; 12.5% (2) the anterior one-half to three-fourths of the tongue; 43.7% (7) tongue and one eye; 6.3% (1) tongue and both eyes; 6.3% (1) tongue, one eye and part of the intestinal tract (entry through a scavenger-made hole in the anal area); and 6.3% (1) tongue, both eyes and parts of the stomach and intestinal tract (entry through about a 6 cm diameter, scavenger-made, intercostal hole). Wolves fed on parts of the remaining 17 of the 34 wolf-killed calves, but determining the extent of the feeding by wolves is complicated by the scavenging of gulls. Although utilization of carcass parts varied, the preferences were for tongues (n = 16) and eyes (n = 15; 13 both eyes and 2 left eye only) and viscera (n = 17; 14 all, and 3 most). All utilization of tongues and eyes was by gulls only. Both wolves and gulls apparently had fed on visceral parts leaving only the lungs and heart in one calf, part of the lungs in another calf, and the kidneys in a third calf. Feeding on deep muscle tissue was minimal by both wolves and gulls and occurred only on 41.2% of the 17 carcasses (n = 7; 7 hindquarters, 5 forequarters, 5 back and 4 rump). Average carcass utilization was 33.8% and less than 50% of 14 of the 17 carcasses was utilized (mean ± SD, 28.2% ± 12.4%; range, 2.6-49.4%). Two carcasses were 53.9% utilized and one 72.7% consumed.

5.2 Suspect wolf predation

Both wolves and gulls had utilized the two suspected wolf-killed calves in 1982 (Tables 18, 20, 21). Both calves had muscle tissue and all viscera removed (Table 18) and they were classified as moderately utilized on a weight basis (Tables 20, 21).

5.3 Grizzly bear predation

No calves (that had been killed by grizzly bears) were found in June 1982.

5.4 Fetal atelectasis

Gulls had scavenged three of the four calves that had died from fetal atelectasis in June 1982. The gulls had not fed on any muscle tissue (Table 17) and had only removed most of the viscera from one of the three carcasses. The latter carcass was classified as heavily utilized (Table 20) whereas the other two carcasses had only lost both or one eye (Table 17) and were classified as minimally utilized (Table 20).

5.5 Neonatal atelectasis

Gulls had scavenged two of the five calves that died from neonatal atelectasis in June 1982. Neither calf had lost muscle tissue (Table 17). Most of the viscera were removed from one calf and it was placed in the moderate utilization class (Table 20). Gulls had fed on only the tongue of the second calf (Table 17) and it was classified as minimally utilized (Table 20).

5.6 Suspect fetal or neonatal atelectasis

No suspect cases of atelectasis were found in June 1982.

5.7 Separation or abandonment (malnutrition/starvation complex)

Gulls had scavenged one of the three calves in this category, and only part of the tongue and an eye had been removed (Table 17). The calf was placed in the minimal utilization category on a weight basis (Table 20).

5.8 Patho-physiological

Gulls had scavenged two of the four calves that had died from patho-physiological conditions in June 1982. The calf classified as heavily utilized on a weight basis (Table 20) had lost some muscle tissue and all viscera (Table 18). The second calf had only had an eye removed (Table 17) and was considered to be only minimally utilized on a weight basis (Table 20).

5.9 Pneumonia

Gulls had scavenged two of the four calves that died from pneumonia in June 1982. One calf had lost some muscle tissue and some viscera (Table 18) but as its weight (7.25 kg) exceeded the mean weight, it was classified as minimally utilized on a weight basis (Table 20). The second scavenged calf which was also classed as minimally utilized, had only its tongue and both eyes removed (Table 17 and 20).

5.10 Unknowns

Wolves and gulls had apparently both fed on 13 of 15 of the carcasses that died from unknown causes in June 1982 and only gulls had fed on the two remaining carcasses. No muscle tissue but all (3) or most (3) of the viscera had been removed from six calves (Table 17). The nine calves which had lost muscle tissue had also had all their viscera removed (Table 18). Most (73.3%, 11/15) of the carcasses were classed as heavily utilized on a weight basis (Table 20). Three calves were classified as having been only lightly utilized on a weight basis (Table 20). The only one unknown classified as minimally utilized (Table 20) was because its weight (7.0 kg) exceeded the mean weight: the calf had in fact lost most of its viscera.

6. Occurrence of Predators and/or Scavengers - 1982

6.1 Wolves

In 1982 we saw only 10 wolves on six occasions: five singles; one group of five.

6.2 Grizzly bears

We saw no grizzly bears on the calving ground in June 1982.

6.3 Gulls

In 1982 the count of gulls (all herring gulls) at each carcass site when the carcass was found was more precise than in 1981. Gulls were at 40 (37.4%) of the 107 calf carcasses when found (Table 23). They occurred as five singles; three pairs; seven groups of 3; seven groups of 4; and five groups of 6. Four additional groups one of 2+, two of 3+, one of 5+ and one group of 8+ had some birds leave the groups before we made our close approach; departing birds could not be accurately counted. Gulls were on all six dead cows when we found them: six groups of 2, 3, 4, 4, 6 and 20 each.

6.4 Minor scavengers

Only one arctic fox was seen in June 1982 and no active fox dens were found. Rough-legged hawks were relatively the most common minor scavengers on the calving ground. Long-tailed and parasitic jaegers were rare; and golden eagles and ravens were even more rare on the calving ground in June 1982.

7. **Case Histories - 1983**

Between 6 and 17 June 1983 we found and necropsied 101 calves (Tables 3, 4, 24) and 11 cows. The sex of 87 of the 101 calves was discernible: 43.6% (44) female; and 42.6% (43) male. The sex of 14 (13.8%) calves was undiscernible. The probability of these values actually representing an even sex ratio was statistically tested. We first assigned the 14 carcasses of unknown sex to the 44 female carcasses to maximize one sex against the other (58 females to 43 males). We then assumed an expected equal sex ratio of 50:50 (101 carcasses/2 sexes) and tested the data with a standard one-way Pearson Chi-square test. The observed value ($\chi^2 = 2.28$, 1df, $P > 0.20$) indicates a likelihood of equal representation by sex in the sample of 101 calf carcasses. The equal representation is in accordance with the expected 'primary or secondary sex ratios' in newborn caribou which suggests that neither sex was predisposed to early deaths in 1983.

All of the calves in the sample were estimated to be less than 1-week-old at death: most, 76.2% (77) had died at <4 d (Table 24). The relatively late peak of calving and our early termination of aerial searches prevented us finding calves that were more than 1-week of age at death in June 1983.

7.1 Causes of calf mortality

We assigned causes of death to 87 calves and eight calves were classified as 'suspect' cases. We classified as 'unknowns' the remaining six calves for which we could not determine the cause(s) of death.

7.1.1 Wolf predation

In June 1983 we determined that wolves had killed 62 calves in the sample of 101 dead calves (Tables 3, 4, 24). Fifty-seven (91.9%) of the 62 wolf-killed calves had fatal head wounds; three (4.8%) calves were decapitated; six (9.7%) the anterior portion of the skull was missing; and the remaining 48 carcasses had punctured, fractured, crushed, or shattered skulls. One (1.6%) of the five calves with no head wounds had been seized by the neck, the other four (6.4%) had fatal wounds to internal organs, and one of these four was still alive when found. We found hemorrhagic or traumatized areas on the bodies of 36 (63.2%) of the 57 carcasses with head wounds which indicated that each calf had been seized several times before being killed. For example, the intact carcass of a 1-3 d old female calf was found on 16 June 1983 (only the right eyeball had been removed by a scavenging gull). The carcass had blood around the ears, the right eye socket, and on the muzzle. Hemorrhagic and traumatized areas were along the right side; on the cervical area, scapula, humerus, abdomen, and femur as well as on the left side of the abdomen. Hemorrhages throughout the thoracic cavity were associated with tooth punctures in the left and right diaphragmatic lobes of the lungs and also the apical lobe was hemorrhaged. The posterior crown of the skull was shattered; there was a tooth perforation posterior to the left eye socket; and the right cerebral cap was shattered, with a fracture line that ran laterally across the skull.

Only seven of the 21 calves with fatal head wounds, but no body wounds had no muscle masses removed, so the lack of body wounds is only accurate for those seven. The extensive feeding on muscle masses of the carcasses of the other 14 calves with fatal head wounds may have obliterated evidence of body wounds.

7.1.1.1 Sex composition

In June 1983, 28 of the wolf-killed calves were males, 26 were females, and only eight were of undeterminable sex. The proportion of female wolf-killed calves did not differ ($\chi^2 = 1.58$, 1df, $P > 0.20$) from the proportion of wolf-killed male calves, when the maximum possible spread by sex is obtained by adding all eight calves of unknown sex to the 28 male calves. The distribution between females and males of the wolf-killed calves in 1983 was almost equal suggesting that calves of neither sex were predisposed to wolf predation because of their sex during their 1st week of life, nor that wolves selected calves by sex.

7.1.1.2 Age composition

In June 1983 we estimated that all 62 wolf-killed calves were <7 d and most (72.6%) were <4 d when killed. Only 13 (21.0%) of the wolf-killed calves were found during the period of highest rate of calving in June 1983 (one, 7 June; one, 10 June; four, 11 June; two, 12 June; and five, 13 June), and all were 1-3 d old at death. The remaining 49 (79.0%) wolf-killed calves were found between 15 and 17 June during the early postcalving period. Of those calves, 32 (65.3%) were <4 d old at death and 17 (34.7%) were 4-7 d old. The occurrence of 1.9 <4 d old calves among the wolf-killed calves to every one 4-7 d old calf argues for wolves definitely selecting younger calves in mid June; or that more calving probably took place after 12 June 1983 than we thought; or that late born calves were more vulnerable to wolf predation.

The significant difference ($\chi^2 = 12.56$, 1df, $P < 0.001$) between the proportion of younger (<4 d, 72.6%) and the proportion of older (4-7 d, 27.4%) calves killed by wolves in June 1983 also indicates that wolves took proportionately more <4 d old calves than would be expected by chance alone. Empirically, younger (<4 d) calves would be likely more prone to being taken by wolves than older (4-7 d) calves. The apparent, condition could also, however, simply reflect a greater proportion of calves present that were <4 d old than 4-7 d old calves during the search period in June 1983. Therefore we looked at the age distribution of calves during the search period in 1983. If we assume that about 90% of the calves were born by 14 June and calving progressed from 8 June to 14 June at about an even rate of 12% per day from a start of about 18% (based on percentage of cows seen with calves) on 8 June, we find the following:

(1) Only about 42% of the calves would have been 7 d of age or older on 17 June.
(2) About 66% of the calves would have been about 5 d old or older on 17 June (sufficiently into the 4-7 d old class that they likely would have been judged to have been 4-7 d old at death).
(3) All 90% of the calves would have been 3 d old or older on 17 June.

Therefore, only the calves born before 8 June could be 4 d old or older by 11 June; and those calves should have represented, at most, about 33% (18%/54%) of the calves alive on 11 June. However, by 15 June, when the first wolf-killed 4-7 d old calf carcass was found, there should have been at least a 50:50 chance that one out of every two calves alive was 4-7 d old (54%/90% = about 60% 4-7 d old or older). Only 13 wolf-killed calves were found before 15 June, and all were estimated to be <4 d old at death. All 17 of the 4-7 d old wolf-killed calves in the sample were obtained between 15 and 17 June 1983.

We also found 32 wolf-killed calves <4 d old during the same time period (15-17 June). Therefore, we did a one-way Chi-square test of the 32 calves (<4 d) against the 17 calves (4-7 d), assuming equal representation at 24.5 calves. The value was significant ($\chi^2 = 4.70$, 1df, $P < 0.05$), which allows us to accept that, in June 1983, wolves took proportionately more younger calves (<4 d) than they did older calves (4-7 d). The data then indicate that newborn caribou calves are vulnerable to wolf predation throughout at least the first week of life, and are especially vulnerable when the calves are <4 d old.

In 1983, 19 (30.6%) of the 62 carcasses from wolf-killed calves had lung tissue present. The lungs from one (5.3%) calf had a pneumonic condition and the calf's death could be considered compensatory. One calf with normal lungs had an abscess in the liver, with adhesions between the liver and the diaphragm. Hemorrhagic areas in the liver and the lungs suggested that the liver was probably traumatized by the calf being stepped on by the maternal or a strange cow. Two other calves with normal lungs had scours caked to their anal area, and one calf (no lungs left) also had scours caked to its anal area. The remaining 42 (67.8%) carcasses had no lung tissue left and showed no evidence of any physiological or pathological conditions that would have made them vulnerable to wolf predation.

In 1983 the locations of the wolf-killed calves that we found (assuming that we did not miss adjacent kills at single finds) suggested that 71.0% (44) were in clumped associations (Table 25). Within-clump-distances were for the individuals in the clump of eight, 50 to about 500 m; clump of six, 5 to 500 m; and clump of five, 100 to 500 m. The individuals in the second clump of five were within 200 to 500 m of each other; those in the clump of four, 20 to 300 m; those in the two clumps of three, 50 m and 300 m; and those in the five clumped pairs, 1, 5, 50, 200, and 200 m.

7.1.2 Suspect wolf predation

In June 1983 we found the partial carcasses of three calves that we believe were killed by wolves (Tables 4, 24). Two of the carcasses were found on the same day within several hundred metres of each other and in the same area as the carcasses of eight wolf-killed calves. One of the calves, a 4-7 d old of undiscernible sex, had the general appearance of a calf that was killed and extensively fed on by wolves. One hind leg and one foreleg were about 3 m from the carcass; only a few tatters of the hide were left from head to tail; the left humerus was severed; the right foreleg was disarticulated at the sternal joint; all ribs were severed at about mid-point; and the spinal processes were severed. The other carcass, a 1-3 d old female calf, was sprawled about 3 m above a snowbank on the edge of a lake. A wolf had apparently bitten through the right rib cage, and the carcass' appearance was suggestive of a wolf mauling.

The third carcass was from a 4-7 d old calf of undiscernible sex that had traumatized areas on the left hind leg, the dorsal portion of the left paralumbar fossa, and the left withers. The carcass was found on the same day along with six wolf-killed calves in one general area. A wolf had apparently fed on the carcass, which was lying at the base of a steep slope in a small stream.

7.1.3 Grizzly bear predation

In June 1983 we did not catalogue any calf as having been killed by grizzly bears. However, we found a partial carcass of a <1 d old calf of undiscernible sex piled alongside its maternal cow who had been killed and cached by a grizzly bear. The calf remains were the hind legs, joined together at the pelvis by skin only; the spinal column with ribs attached, but ribs separated from sternum; the forelegs held together only by skin; and pieces of the skull. The calf had not been completely cleaned by its mother before her death. Therefore, we considered the cause of death of the calf questionable (and by oversight, it was not added to the numbered cases of undiscernible deaths - 'unknowns').

7.1.4 Fetal atelectasis

We termed the essentially intact carcasses of five stillborn calves found in June 1983 to be the result of fetal atelectasis (Tables 3, 4, 24). The lungs of all five calves had totally failed to convert from fetal lung tissue to functional neonatal lungs. Three of the calves had been only partially cleaned by their mothers; placental remnants were adhering to the pelages and there were patches of sticky or dried amniotic fluids on the pelages. The total lack of any wear and the soft cartilaginous tips of the hooves indicated that none of the calves had ever walked.

The three females had all obtained viable weights (6.0, 5.5, and 5.25 kg). The two males each weighed a nonviable 3.5 kg. One of the male carcasses had been cleaned of afterbirth, but the other still had placental tissue adhering. The latter carcass had a bloody, gelatinous, hemorrhage on the left femur in the area of the lumbar fossa, in the right cervical area and diffused over the skull cap, below the left mandible and left ethmoid bone. The skull was severed in about the area of the ethmoid bones, probably from being stepped on by the maternal cow in an attempt to elicit a response to her care-giving behaviour. The gelatinous hemorrhagic condition is more typical of maternal circulation and together with the flaccidity of the calf's heart suggest the fetus had remained on the mother's circulatory system.

One of the carcasses (5.25 kg) from the three female stillborn calves was wet with sticky amniotic fluid along its back. It had a small hemorrhage associated with its umbilicus. Its liver had pale areas, typical of fetal liver, but the good muscle tone of the heart suggested independence of maternal circulation. The second female carcass (5.25 kg) had amniotic fluid and placental tissue on its right side, belly, and forelegs as only its left side, head, and hindlegs were cleaned. It also had a hemorrhage in association with its umbilicus (the umbilical cord had been snapped short) and its heart had good muscle tone. The third carcass (6.0 kg) of a female calf had been completely cleaned off. Its heart had good muscle tone, but the calf was still lying on what was, most likely, its birth site - a scuffed and flattened area with tufts of caribou winter hair.

7.1.5 Neonatal atelectasis

We determined that two essentially intact <1 d old male calves in June 1983 had died of neonatal atelectasis (Tables 3, 4, 24). The whole body weight of one calf was a nonviable 3.75 kg and the essentially whole body weight of the other was a threshold weight of 4.0 kg. The former calf had milk curds in its stomach and the latter had an empty stomach. Neither calf had ever walked enough to show wear on their hooves. The extent of atelectasis in the lungs of the light calf ranged from about 90% in the right and 20% in the left diaphragmatic lobes to 5% in the apical lobe. The range was about 90% in the left, 80% in the right diaphragmatic lobes and absent from the apical lobe of the lungs of the second carcass.

7.1.6 Suspect fetal or neonatal atelectasis

We could not fully determine the causes of death for the partial carcasses of five calves found in June 1983 as the lungs were missing (Tables 4, 24). We would classify them as suspect fetal rather than neonatal atelectasis for the following reasons.

(1) All had no sign of wear on their hooves with soft cartilage ends still in place, indicating that they had never walked.
(2) One female calf had been born probably to a cow with dystocia. The calf had areas partially denuded of hair: one area about 6x6 cm posterior to the left elbow, one about 5 to 9x6 cm on the right side of the rib cage, and one about 3 to 5x5 cm in the right paralumbar fossa area. It also had small hemorrhages where the hair was denuded on the upper right femoral area. It was the only one of the five carcasses still with a stomach that was empty.
(3) Two other carcasses (female and male) were found lying probably on their birth sites; areas of scuffed and flattened vegetation with considerable amounts of caribou winter hair. One of those two carcasses still had remnants of placental tissue on the inner left thigh and the left side of the body was still sticky with amniotic fluids. The presence of the meconium in the gut meant it had probably not nursed. The other one of those two carcasses had placental mucus in the mouth and a nearby cow, probably its mother, was feeding on afterbirth.
(4) The fourth carcass (male) still had the meconium present in the gut, suggesting it had never fed.
(5) The fifth carcass (sex unknown) had relatively pale pelage; the carcass was small boned with a relatively large skull, the front of which (the face) was dished in a manner typical of hydrocephalus. We suspected atelectasis as the proximal cause of death as the calf had not been cleaned off.

7.1.7 Separation or abandonment (Malnutrition/starvation complex)

We found the carcasses of eight calves (five females, two 1-3 d, three 4-7 d; three males, one <1 d, two 1-3 d) that had become separated from or abandoned by their mothers and then had died from a malnutrition/starvation complex in June 1983 (Tables 3, 4, 24). Six of those calves (five females, one male) also had pneumonia which contributed to their deaths (Table 26).

The partial carcasses of two male calves had no sign of pneumonia. One had only a trace of vegetation in its stomach. The other carcass had no stomach remaining, though the large size of the hind gut indicated that the calf had been recently feeding on only vegetation.

All six of the carcasses with pneumonia were essentially intact and whole body weights averaged 5.3 ± 1.02 kg standard deviation (range 3.75 to 6.5 kg). The stomachs from two of those calves were empty, two had only traces of vegetation, and two had a little vegetation in them.

All five carcasses from female calves exhibited some additional evidence of other possible patho-physiological problems.

Two carcasses had bloody fat around the kidneys suggestive of fat utilization. One of those two carcasses also had an abraded patch on the skin in the left lumbar area. A third carcass had hemorrhages associated with the pericardial sac and the lungs were quite red - possibly the results of panicky respiration. A fourth carcass had a small trauma anterior to the umbilical cord, and had no fat around the kidneys. A fifth carcass had a small hemorrhage on the inner canthus of the right eye.

One of the carcasses from the three male calves had no fat around the kidneys and a small amount of scours around the anus, probably caused by poor nutrition. There was still fat on the kidneys in the carcasses from the other two male calves.

7.1.8 Patho-physiological

We found seven calves that had died from patho-physiological conditions in June 1983 (Tables 3, 4, 24). Six of the seven carcasses were intact. The carcasses of one female and three males were all aged 1-3 d and were lying in the water: their whole body weights (wet) were 4.5, 4.0, 5.25, and 6.0 kg, respectively. An additional female (1-3 d) and another male (1-3 d) were dry and weighed 5.5 kg and 4.75 kg, respectively. The seventh carcass (female, 1-3 d) was partially scavenged.

Six calves apparently drowned, or died from shock, or other stress while trying to cross slushy areas along the shores of lakes. The areas where the carcasses were about 10-30 m out from shore where the slush often approached 50 cm in depth before grading up into shallower, thicker slush; then into non-supporting, heavy, wet, deep snowbanks closer to and onto the shores. These conditions had been brought on by a sudden warming trend that persisted from the second week of June onward. We saw live calves in these slush mires on several occasions; their maternal cows stood next to them, encouraging the exhausted calves to move. We did not see, however, a cow physically try to push her calf from the mire. On four other occasions, we saw cow-calf pairs bedded on lake ice or just on shore only a few metres from where the calves had apparently been entrapped in the slushy mire. Twice we saw maternal cows actually bedded down in the slush next to their entrapped calves.

We found a cow still standing over the carcass of a calf on three occasions. There were 6-8 fecal pellet groups at a fourth carcass, suggesting that the maternal cow had remained for some time with her calf.

One of the six calves had drowned and its maternal cow was standing nearby on the ice in 8-10 cm of slush at the edge of a snowbank on an island shore. The calf had a considerable amount of fluid in the lungs, froth in the trachea, patches of necrosis on the liver (origin unknown), but the heart had good muscle tone. The carcass of the second calf was floating in about 50 cm of water at the end of a deep snowbank coming off an island shore. The calf had probably drowned though no fluid could be expressed from the lungs or trachea, some lung tissue was pale and frothy. This calf also had zonal necrosis on its liver.

The remaining four of the six calves died from shock or other stress related complications rather than drowning. The first of these four carcasses was lying in 10-20 cm of icy slush 6-7 m from the shore of a lake. This carcass had traumatized and hemorrhagic areas especially on the left stifle joint but also along the anterior surfaces of the forelegs - most likely caused by the calf fighting the broken ice in the slush. The intestinal tract was hemorrhagic, which might have been related to the shortness of the umbilical stump. The kidneys were pale - which is unusual in young animals. The kidneys were, however, well fatted and the calf was generally in good physical condition.

The carcass of the second of these four calves was lying in about 45 cm of icy slush 6-7 m out from the lake shore. The carcass also had traumatized subcutaneous hemorrhagic areas on the stifles, knees, and dorsal area of the left humerus - indicative of its struggles to free itself from the slush mire. The kidneys were well fatted and the calf was generally in good physical condition. The third carcass of these four was floating in about 45 cm of ice-free overflow on the lake. However, no fluid could be found in the lungs. The liver was mottled with necrotic patches. Yellowish scour-like material and flatulence in the intestines was typical of Escherichia coli. There was substantial fat on the kidneys. The fourth carcass of these four was spreadeagled on an ice-shelf at the base on a snowbank on an island shore. There was a small trauma on the left stifle and the skin was denuded between the shoulders. The lungs were pale but had no fluid in them. The liver had patches covered with necrosis. There was substantial fat on the kidneys.

The carcass of the seventh calf that died from a pathophysiological condition had a ruptured liver. Most likely the calf's death resulted from it being trodden on by the maternal or another cow. It was lying on its flank at the edge of a small island just above the snow on the lake. There was extensive hemorrhaging throughout the abdominal cavity in association with the ruptured liver.

7.1.9 Pneumonia

We found the carcasses of three calves that had died from pneumonia in June 1983 (Table 3, 4, 24). Two of the carcasses were essentially intact: one 1-3 d female (5.75 kg) and one 1-3 d male (6.5 kg). The female had marked discoloration (pale) of the intercostals, gluteus maximus, and biceps femoris - suggestive of a muscular dystrophy. The male had no fat around the kidneys and a small amount of scours around the anus, probably caused by lack of good nutrition. The third carcass was from a 1-3 d male calf which although extensively scavenged, still had most all of the lungs present.

Percentage distributions of the pneumonic patches in the lobes of the lungs varied among carcasses (Table 26). The variation in the coverage of pneumonic patches in the lungs was more extreme when compared with the six calves classified as cases of separation or abandonment (malnutrition/starvation complex) that also had pneumonic conditions (Table 26).

7.1.10 Unknowns

We could not discern cause(s) of death for the partial carcasses of six calves in June 1983. All of the carcasses were scavenged and most of the sites, body parts, or organs where much of the evidence for probable cause(s) of death would be found were missing. Only one carcass (male) had signs of induced trauma: it had a contusion and trauma associated with the sternum; and blood in the trachea. The other five carcasses (two female, three unknowns) had no punctures, hemorrhages, or traumas.

7.2 Causes of cow mortality - 1983

In June 1983 we found 15 dead cows and only necropsied 11 of them. We could not examine the carcasses of three of the cows because they were submerged in lakes and a fourth carcass was too decomposed. All three of the submerged carcasses were too fragmentary for detailed examination. Apparently, they had died in May on lake ice and had been extensively fed on by predators or scavengers before sinking into the water. The 11 cows necropsied ranged in age from 3 to 7-8 yr old.

7.2.1 Wolf predation

We determined that seven (63.6%) of the 11 cows were killed by wolves. Three of those seven cows had calved already and four were still pregnant when they were killed.

The first carcass, a 4-5 yr old cow, was lying on a small island at the edge of a snowbank leading to the lake ice (the area had large boulders throughout it). Her stillborn female calf was sprawled on the ground about 2 m from the cow. The cow's neck had been ripped open from the base of the throat between the mandibles posteriorly for about 25 cm. The neck had tooth puncture wounds in it and the tissues were traumatized and hemorrhaged. The left mandible was fractured at the diastema; and the posterior section of the tongue and the hyoid apparatus were removed, apparently by a wolf. The skin of the cow's tail had been pulled off, leaving the bones and flesh. The marrow of her femur was firm and waxy to the touch and whitish in appearance. The left eye had been scavenged by a gull, but there were no gulls near the carcass when found.

The second carcass, a 5-6 yr old cow, was lying 6-7 m from the top of a steep, deep snowbank, down which was a deeply furrowed caribou trail. The remains of a wolf-killed 1-3 d old female calf were only 3-4 m from the cow. The base of the cow's throat had been torn open and the tongue and the hyoid apparatus were missing, but the mandibles were still intact. The cow's neck had tooth puncture wounds in it and the tissues were traumatized and hemorrhaged. Her left hind leg also had tooth punctures and the tissues were hemorrhaged. The carcass had been fed on by both wolves and gulls. Entries to the abdominal cavity had been gained through the abdomen and flank, and gulls had pecked holes in the anal area. The right eye, liver, stomach, kidneys, intestinal tract, and muscle masses from the pelvis and femurs were missing. The marrow of her femur was firm and waxy to the touch and whitish in appearance. There were two gulls and one rough-legged hawk on the cow's carcass when we landed.

The third carcass, a 5-6 yr old cow, was lying at the edge of a small pond. She apparently calved elsewhere, as no calf was found in the area. The cow's throat was ripped open from the base of the neck to the posterior end of the mandibles; the heels of the mandibular blades were fractured off; and part of the tongue and the hyoid apparatus were missing. The marrow of her femur was firm and waxy to the touch and whitish in appearance. The carcass had been utilized by both wolves and gulls. Entries to the body cavities had been gained through the rib cage, abdomen, and flank. The left eye, lungs, heart, liver, stomach, kidneys, intestinal tract, and parts of the flank and hindquarters were missing. There were no gulls present when found.

The fourth carcass, a 5-6 yr old cow, was lying about 200 m out on the lake ice from an island. A gull's egestus was lying next to the cow's carcass, containing a fetal mandible and pieces of bone and hair from a fetus. The cow's neck had been ripped open from the base of the throat to the base of the neck; the tongue was gone, but the hyoid apparatus and mandibles were still intact; and there was frank blood in the mouth and in the nasal passages. The cow's neck had tooth puncture wounds in it and the tissues were traumatized and hemorrhaged. The marrow of her femur was firm and waxy to the touch and whitish in appearance. The cow had besnoitiosis. The carcass had been fed on by both wolves and gulls. The flank was opened and the three posterior right ribs were exposed; all of the viscera were removed, except about 20 cm of intestinal tract; and the muscle masses were removed from the pelvis and femurs. The carcass had also been scavenged in the anal area and holes had been pecked along the back. There were no gulls on or near the carcass when found.

The fifth carcass, a 6-7 yr old cow, was lying 6-7 m from the top of a snowbank on an island shore. The skull cap, vertebral column, and one hind leg of a fetus were lying about 5 m from the cow. The cow's throat had been ripped open; the tongue was gone, but the hyoid apparatus and mandibles were still intact. The cow's neck had tooth puncture wounds in it and the tissues were traumatized and hemorrhaged. Her left humerus also had tooth punctures in it and the tissues were extensively traumatized. The marrow of her femur was firm and waxy to the touch and whitish in appearance. The carcass had been fed on by both wolves and gulls. Entry to the abdominal cavity had been gained through the flank and gulls had pecked holes in the anal area. The right eye, lungs, heart, liver, stomach, kidneys, intestinal tract, flank, and parts of the hindquarters and forequarters were missing. There were two gulls on the carcass when found.

The sixth carcass, a 6-7 yr old cow, was lying on lake ice; the ribs had been pecked clean of tissue, but were still articulated. We found one fetal foreleg and a piece of fetal hide on the lake ice about 100 m away. The cow's throat had been ripped open from the base of the throat to the base of the neck; the tongue was gone, but the hyoid apparatus and mandibles were still intact. Much of the muscle masses of the neck had been removed and there was clotted blood and trauma in the remaining tissues and on the skin. The marrow of her femur was firm and waxy to the touch and whitish in appearance. The carcass had been fed on by both wolves and gulls. Entries to the abdominal cavity had been made through the rib cage, abdomen, and flank. Both eyes, lungs, heart, liver, stomach, kidneys, intestinal tract, and part of the flank were missing. There were no gulls on or near the carcass when found.

The seventh carcass, a 7-8 yr old cow, was lying at the base of a snowbank at the edge of an island near the lake ice. She was still carrying a male fetus in her uterus. The cow's throat had been ripped open from the base of the neck to the base of the throat; the tongue was gone, but the hyoid apparatus and mandibles were still intact. The neck had tooth puncture wounds and the tissues were traumatized and hemorrhaged. There were also hemorrhages in the cow's mouth and nostrils, and a hole in her chest with her trachea sticking out. The marrow of her femur was firm and waxy to the touch and whitish in appearance. The carcass had been fed on by both wolves and gulls. Entry to the abdominal cavity had been gained through the abdomen. Gulls had pecked holes along the spine, in the left femur, and in the anal area (part of the vagina was hanging out). There were no gulls on or near the carcass when found, but there were two gulls seen on the carcass the following day.

7.2.2 Grizzly bear predation

We determined that three of the four remaining 11 cows were killed by grizzly bears. Two of them had apparently already calved in 1983 and the third was parturient.

A grizzly bear was sitting by the carcass of a 3-yr-old cow, that was at the base of a slope on a large snow patch. Lichens, soil, and litter had been scraped over the carcass, mostly hiding it from sight. The calf's remains laid piled together beside the cache mound. The throat and neck of the cow had been ripped open, and the tongue was gone. The neck had tooth puncture wounds in it and the tissues were traumatized and hemorrhaged. The face anterior to the palate was severed from the cranial vault, but was held together by skin. The nasal and turbinate bones were intact and there was no blood in the nostrils. The carcass had a traumatized area on it from the left lumbar area to the left scapula. The viscera were intact, except for the rumen which was opened and part of the intestinal tract which was missing. The abdomen was ripped open to the anus. The marrow of her femur was firm and waxy to the touch and whitish in appearance. The carcass had been fed on by the bear, but apparently the bear had kept the gulls from feeding. There were two gulls near the carcass when found.

The second carcass, a 5-6 yr old cow, was lying on a snowbank in a flat area about 3 m from the edge of a lake. Lichens, soil, and litter had been scratched up over the carcass, and the guts were piled about 1-m away. The carcass of a 4-7 d old female calf that died apparently of a malnutrition/starvation/pneumonia complex was found about 100 m away from the cow. The cow's throat had been ripped open to the chest, and there were tooth puncture wounds in the hemorrhaged tissues of the neck. Her skull was severed at the orbits; the nasal and turbinate bones were still intact, but attached only to the skin of the head. The hind legs, though disarticulated were attached to the body by the skin; the left femur was shattered, and the head of the femur was bitten off. The heart was intact in the chest cavity, but 90% of the lungs were missing. The marrow of her femur was firm and waxy to the touch but pinkish-white in appearance. The carcass had been fed on by the bear and by gulls. Entry was gained to the abdominal cavity through the abdomen. Some muscle tissues had been removed from the femurs and the rump. There were 10 gulls near the carcass when found, but they were not actively feeding on it when we approached and landed.

The third carcass, also a 5-6 yr old cow, was lying on the ice of a small pond about 10 m from the base of a steep esker (deep snowbank on face of esker). A fetal skull cap and both hind legs of a fetus were lying about 10 m from the cow's carcass. The cow's head was disarticulated and lying beside her carcass. Her nasal and turbinate bones and the anterior part of her maxillae were severed; her mandibles were separated; and the tongue and shafts of the mandibular blades, including incisors, were missing. All four legs were disarticulated but still attached to the carcass by the hide. The marrow of her femur was firm and waxy to the touch and whitish in appearance. The carcass had been fed on by the bear and by gulls. Entries to the body cavities had been gained through the rib cage, abdomen, and flank. The lungs, heart, liver, stomach, kidneys, intestinal tract, and part of the flank were missing. Most of the muscle masses had been removed from the femurs, humeri, and scapulae. The left eye had been plucked and the rib cage pecked clean of most of its tissues by gulls. There were no gulls on or near the carcass when found.

7.2.3 Birth complications and associated diseases

We determined that only one of the 11 cows had died from complications associated with giving birth: a 3-yr-old died from peritonitis, caused by a prolapsed uterus. The carcass was bleached out and the cow appeared to have been dead for some time before being found. There was extensive peritonitis throughout the abdominal cavity, with the prolapsed uterus protruding from her vagina. The marrow of her femur was firm and waxy to the touch and whitish in appearance. The carcass had only been scavenged lightly on the upper right foreleg, probably by an Arctic fox. There were no signs of scavenging by gulls, and there were no gulls near the carcass when found.

8. Carcass Use by Predators and/or Scavengers - 1983

In June 1983 we obtained whole body weights from the carcasses of 33 calves, all 1-week or less of age at death. However, six carcasses were water-soaked, and thus their weights were inflated. Also, four carcasses weighed less than 4.0 kg (2, 3.5 kg; 2, 3.75 kg) our arbitary minimal threshold weight for viable calves. Therefore, we used only the weights from the remaining 23 carcasses to calculate average viable whole body weights in June 1983 (Table 27).

In 1983 85.1% (86) carcasses of the 101 calves, all <7 d old at death, were fed on by wolves (one possibly by an arctic fox only) or gulls (Tables 28-32). Eighteen of those 86 carcasses had less than 0.25 kg of tissue removed (essentially just tongues and eye(s)). Those 18 carcasses were used as whole body weights in the set of 23. The total weight of those remaining 68 carcasses should have been about 369-390 kg but the measured total weight for them was 244 kg. Therefore, the range of estimated utilization of those 68 carcasses amounted to 34-37% (369 - 244/369 and 390 - 244/390). In 1983 the rate of utilization among carcasses varied considerably (Tables 8, 9, 31, 32). Only 19.8% of the carcasses on a percentage utilization basis received more than 50% utilization (Table 9).

In 1983, 79.1% (68) of the 86 carcasses fed on by predators or scavengers had visceral parts missing: 51 (75.0%) had all viscera taken; and 17 (25.0%) had most or only some visceral parts gone (Table 28). Five (29.4%) of the 17 carcasses with some visceral parts remaining had the stomachs present which were all full of milk curds. All five of the carcasses had been scavenged by gulls but showed no signs of having been fed on by wolves. Lungs, liver, (partial or whole) and kidneys were the organs most frequently left in the carcasses in 1983.

In 1983, only 36.0% (31) of the 86 carcasses fed on by predators or scavengers had deep muscle tissue removed (Table 29). Only 48.4% (15) of them also had all (53.3%), most (20.0%), or just some (26.7%) of the viscera removed (Table 29).

All but two of the 65 carcasses of calves killed by wolves (n = 62) or suspected to have been killed by wolves (n = 3) in June 1983 were either subsequently fed on by wolves and gulls (n = 38, 58.5%) or scavenged by gulls (n = 62, 95.4%). Only one carcass fed on by a wolf had not been scavenged by a gull. Also, 17 of the carcasses of the 30 calves that died from non-predator causes and all six carcasses of the calves that died from unknown cause(s) were scavenged by gulls (but apparently not fed on by wolves). We found no evidence of wolves scavenging on any of the carcasses of calves or adult cows in June 1983. Percentages of carcass utilization were greatest for the carcasses of wolf-killed calves that apparently were both fed on by wolves and scavenged by gulls, and least for carcasses of calves that died from non-predator causes (Table 9).

8.1 Wolf predation

We judged that 35 of the 62 carcasses of wolf-killed calves were fed on by wolves and scavenged by gulls, 24 carcasses were scavenged by gulls only; an additional carcass was fed on by a wolf only and the remaining two carcasses were not utilized (Tables 32, 33). Utilization of individual carcasses varied from 1-9% to about 90% utilized and overall utilization of individual carcasses was low (Table 32). Expected total body weight of the 62 wolf-killed calf carcasses should have been about 336-356 kg. The measured value for those 62 carcasses was 245.25 kg, which suggests that on a weight basis only about 27 to 31% of the 62 carcasses were utilized by wolves or gulls (336 - 245.25/336 and 356 - 245.25/356).

8.1.1 Carcass handling and utilization by both wolves and gulls

We determined the points of body entry by wolves or gulls into the thoracic or abdominal cavities of wolf-killed calves for 29 of the 35 carcasses that were fed on by wolves and scavenged by gulls (Table 30). The six remaining carcasses were too heavily utilized to determine the original points of entry to the body cavities. All 29 carcasses had thoracic or abdominal entries through the rib cage, 23 (79.3%) had entries through the flank, and 22 (75.9%) through the abdomen. Twenty-eight of those 29 carcasses had some ribs broken, severed, or separated. Body cavity entries involving the rib cage in 26 of the carcasses appeared to have been made by wolves. Posterior ribs separated from the sternum in two of the remaining three carcasses appeared to have been caused by the rib cages drying out. However, entries in the rib cages of those two carcasses were also associated with apparent wolf entries through the abdomens and flanks, which could have weakened the sternal articulations of those ribs. Only one carcass had an intact rib cage; a scavenging gull entered the thoracic cavity through an intercostal hole and wolf entry was through a hole in both the abdomen and flank. The entries in 28 carcasses with damaged rib cages were all associated with larger areas of apparent wolf-entry through the flank and/or abdomen. Body entries in those 28 carcasses were through the rib cage, abdomen, and flank 53.6% (15) of the time; through the rib cage and flank 25.0% (7) of the time; and through the rib cage and abdomen 21.4% (6) of the time.

Thirty (85.7%) of the 35 calf carcasses utilized by both wolves and gulls had all or part of their tongues removed and 29 (82.9%) had their eye(s) removed by wolves or gulls. The tongue was totally removed from 15 carcasses and only partially gone from the other 15 carcasses. Both eyes were removed from 12 carcasses; only the right eye from another 13 carcasses; and only the left eye from the remaining four carcasses. We believe that gulls removed all or parts of the tongues on 18 (60.0%) occasions by entry through the mouth and the eye(s) on 21 (72.4%) occasions by pecking in the eye sockets. In three (10.0%) of the other cases wolves had apparently removed the tongues: twice by biting into the base of the tongue and ripping it anteriorly between the mandibles, and once by laterally biting off the mandibles and tongue from the head. Nine (25.7%) carcasses had all or major portions of the head bitten off, and we assume that the wolves consumed the tongues on all nine (30.0%) occasions and the eye(s) on eight (27.6%) occasions. One partial skull from these nine carcasses still included the eye sockets, and the eyes had apparently been taken out by gulls (this case is included in the 21 given above).

In six (17.1%) cases gulls had pecked holes in the anal area to gain entry to the abdominal cavity (Table 33). We never saw any evidence to suggest that wolves had gained entry to the abdominal cavity by tearing out muscle tissue in the anal area.

Overall utilization was greatest on the 35 carcasses of wolf-killed calves apparently fed on by wolves and scavenged by gulls [39 to 43%, (190 - 115.25/190 and 201 - 115.25/201)]. The complete viscera were taken with all (n = 9), most (n = 14), some (n = 5), or none (n = 3) of the deep muscle masses from 31 of the 35 carcasses. The other four carcasses had most of the viscera removed along with most (n = 1), some (n = 2), or none (n = 1) of the deep muscle masses. The degree of individual carcass utilization which was highest for these 35 carcasses, ranged from 10-34 to 70-90%: 31% in excess of 50% (Tables 31, 32).

8.1.2 Carcass handling and utilization only by gulls

We determined the points of body entry into the thoracic or abdominal cavities in the carcasses of all 24 wolf-killed calves that we judged were subsequently only scavenged by gulls and not fed on by wolves (Table 33). There were points of entry into the thoracic or abdominal cavities in 19 (79.2%) of the 24 carcasses: 12 (50.0%) times through the flank, 10 (41.7%) times through the rib cage, and six (25.0%) times in the anal area. In nine of those 19 cases, entries to the body cavities were through two separate holes in each carcass: six times in the rib cage and the adjacent flank, twice in the flank and the anal area, and once in the rib cage and the anal area. The remaining five carcasses had no entries into their body cavities but their tongues or eye(s) had been removed: the tongue and eye(s) of three, tongue only of one, and eye(s) only of one.

The tongue was taken from 21 of the 24 carcasses: totally removed in four cases and partially removed in the remaining 17 cases. The eye(s) were taken from 18 of the 24 carcasses: both eyes in three cases, the right eye in another nine cases and the left eye in the remaining six cases.

Overall utilization of the 24 carcasses of wolf-killed calves that were only scavenged by gulls ranged from 12 to 17% (130 - 114/130 and 138 - 114/138). All of the viscera were taken along with all (n = 1), most (n = 5), some (n = 1), or none (n = 2) of the deep muscle masses from nine of the 24 carcasses. Two other carcasses had most of the viscera missing along with some (n = 1) or none (n = 1) of the deep muscle masses. Another three carcasses had some of the viscera gone and no deep muscle masses removed. Eight of the remaining 10 carcasses that had no viscera taken, had no deep muscles removed and two had some deep muscle masses missing. The degree of individual carcass utilization was markedly lower for these 24 wolf-killed carcasses, 1-9% to only 35-49%, (Table 32) compared to the 35 wolf kills fed on by wolves and gulls.

The two marked differences observed in 1982 between the pattern of points of entry into the body cavities of carcasses of wolf-killed calves scavenged only by gulls persisted in 1983.

(1) There were no abdominal entries by gulls only.
(2) There were no single entries by gulls involving more than one site in combination. That is, all carcasses that were scavenged by gulls only with entries in both the rib cage and flank had separate holes in those areas rather than one continuous hole as in carcasses that apparently were both fed on by wolves and scavenged by gulls.

8.1.3 Carcass handling and utilization only by a wolf

The carcass of a wolf-killed calf that apparently was fed on by a wolf only, but not scavenged by gulls, was 22 to 26% utilized (5.42 - 4.25/5.42 and 5.74 - 4.25/5.74). The use of the individual carcass fell in the 10-34% class (Table 32).

8.2 Suspect wolf predation

Gulls and wolves had apparently both fed on the three carcasses of suspected wolf-killed calves in June 1983. Muscle tissue and all the viscera had been taken from the three carcasses (Table 29). Estimated carcass utilization on a weight basis was 34-38% (16.3-10.75/16.3 and 17.2-10.75/17.2). On an individual carcass basis the level of utilization ranged from heavy for one carcass which had been dismembered to light for the other two carcasses (Table 31).

8.3 Grizzly bear predation

The one (uncatalogued) partial carcass was estimated to weigh 1-1.5 kg. The viscera, most muscle and most of the head was missing.

8.4 Fetal atelectasis

Gulls had scavenged only two of the five calves that had died from fetal atelectasis in June 1983. Neither calf had muscle tissue or viscera removed; one carcass had lost an eye and the other had both eyes and the tongue taken (Table 28). Both calves were in the minimally utilized class (Table 31).

8.5 Neonatal atelectasis

Gulls had scavenged only one of the two calves that died of neonatal atelectasis in June 1983 and the gulls had only taken half the tongue and both eyes (Table 28). The calf was classified as minimally utilized (Table 31).

8.6 Suspect fetal or neontal atelectasis

Gulls had scavenged all five calves that were suspected to have died of atelectasis. Muscle tissue had not been removed from two carcasses that had all and some of the viscera removed, respectively (Table 28). The three carcasses that had muscle tissue removed had lost all (2) or most (1) of the viscera (Table 29). Two of the carcasses were heavily utilized, two were moderately utilized, and one was lightly utilized (Table 31).

8.7 Separation or abandonment (malnutrition/starvation complex)

Gulls had scavenged five of the eight carcasses in this category in June 1983. Three carcasses had no muscle or viscera removed though each had an eye taken (Table 28). The two carcasses with some muscle tissue missing had also lost most or some of the viscera (Table 29). As the weight of the carcass (8.5 kg) with most of the viscera taken exceeded the mean weight, it was assigned to the minimal utilization class on a weight basis (Table 31). The other four scavenged calves were also classified as minimally utilized (Table 31).

8.8 Patho-physiological

Gulls had scavenged only two of the seven calves that died from patho-physiological causes in June 1983. The gulls had taken only an eye from one carcass and muscle tissue and some viscera from the second carcass (Tables 28 and 29). The two carcasses were assigned to the minimal utilization class (Table 31).

8.9 Pneumonia

Gulls had scavenged two of the three carcasses that died from pneumonia in June 1983. Gulls had only removed part of the tongue from one calf (Table 28) but had taken muscle tissue and most the viscera from the second calf (Table 29). The latter calf was classified as lightly utilized and the former as minimally utilized (Table 31).

8.10 Unknowns

Gulls, though apparently not wolves, had scavenged all six calves whose cause of death was not discerned. Only two carcasses did not have muscle tissue removed though all or most of the viscera were taken (Table 28). Three of the four carcasses with missing muscle tissue had all the viscera taken and the fourth carcass had most of the viscera taken (Table 29). Three of the carcasses were heavily utilized, two were moderately utilized, and one was lightly utilized (Table 31).

9. Occurrence of Predators and Scavengers - 1983

Our limited sightings of wolves and grizzly bears suggested that rates of occurrences were low. Herring and glaucous gulls, were the most common scavengers and arctic foxes, rough-legged hawks and jaegers (mainly long-tailed and some parasitic) were minor scavengers. No eagles or ravens were seen.

9.1 Wolves

We saw only three solitary wolves during our helicopter flying over the calving ground in June 1983. We identified them as different individuals because of variations in the colour patterns of their pelages. A fourth wolf was seen at a tent camp on the west side of Deep Rose Lake (H. Miles, pers. comm.).

One of the three wolves seen from the air was lying in a wet sedge (Carex spp.) meadow, and was not displaced by the helicopter flying by at several hundred metres distance. The wolf was spotted by an observer who was glassing an aggregation of postcalving cows and their calves, that was about 100 m beyond the wolf. As the wolf remained lying down on the ground, we thought it was on a kill, so we turned back to investigate. As the helicopter came within 100 m or so the wolf rose and ran off, paralleling the group of caribou (that was trotting off in response to the helicopter also coming closer to them). We lost track of the running wolf as we concentrated on keeping track of the site where the wolf had been lying down, because we were interested in finding the kill.

We did not find a kill or any evidence of one having occurred at the site where the overflown wolf had been lying. We concluded that the wolf had been stalking the adjacent group of caribou.

9.2 Grizzly bears

We saw only two grizzly bears during our helicopter flying over the calving ground in June 1983. One bear was sitting next to its cache mound which contained the carcass of a maternal cow, and the carcass of her calf was lying alongside the mound. The other bear was seen galloping across the tundra in response to the oncoming helicopter.

9.3 Gulls

Herring and glaucous gulls were the most common scavengers on the Beverly calving ground in June 1983. Herring gulls were more common than glaucous gulls, although the latter usually occurred in larger groups.

Gulls were still at 23 sites where we found 28 carcasses in June 1983 (Table 34). The sizes of the 23 groups (63 gulls) that were on carcasses averaged 2.7 ± 2.0 (SD) and ranged from 1 to 10 birds in each group. Thirty-five gulls were still on 13 of the 62 carcasses of wolf-killed calves; 31 gulls were still on 11 of the 33 carcasses of calves that died of non-predator related causes. Two gulls were still on one of the six carcasses for which the cause of death could not be discerned. Sixteen gulls were still on four of the 11 carcasses of adult cows: two gulls on one and two gulls on another wolf-killed cow; and 10 gulls on one and two gulls on another grizzly bear-killed cow.

9.4 Minor scavengers

We only saw three arctic foxes on the calving ground in June 1983. Two of those foxes were seen near carcasses; a third carcass had fox tracks around it. We saw a solitary arctic fox on two occasions and heard a fox barking on several other occasions at our base camp just south of the Beverly calving ground.

We saw no active fox dens on the Beverly calving ground in June 1983 (we saw no fresh sign of lemmings anywhere on the calving ground and only two lemmings at our base camp during our ground activities).

Rough-legged hawks were relatively the most common bird of prey on the calving ground in June 1983. We commonly saw one but sometimes two rough-legged hawks at a time while we were carrying out helicopter searches. However, we only saw one solitary rough-legged hawk at two carcasses at the same site: a wolf-killed cow-calf pair.

We saw jaegers, both long-tailed and parasitic, on a few occasions, but never on a carcass. Their numbers appear low enough to be considered rare on the calving ground in June 1983. We saw only one pair of pomarine jaegers, but no golden eagles or ravens on the calving ground in June 1983.

DISCUSSION

We necropsied 287 newborn caribou calves and 23 cows during the 3 years (1981-83) of our study. Our findings underline the importance of wolf predation as the major factor causing early calf mortality. As well as our necropsy results, we discuss the other factors described in the literature that relate to calf mortality such as nutrition of the maternal cows. The effect of weather on calf mortality has been much cited in the literature but in our discussion of the study results we show that the effect of weather may have been overestimated and/or misinterpreted.

Our discussion emphasizes wolf predation as the most important but also the most manageable factor. The proportion of calves killed by wolves in 1981 was lower than in 1982 and 1983. Also, the proportion of calves with head injuries was lower and fewer calf carcasses were in clumped associations in 1981 than in 1982 and 1983. Unfortunately, we cannot fully explain these between-year or among-year differences from our results - the differences are likely the consequences of differences in the hunting patterns of the wolves and/or the distribution of caribou groups in relation to such factors as soft deep snowbanks which increase the vulnerability of the calves. Our sightings of wolves suggest there were relatively few wolves on the calving grounds during our study but nevertheless, the wolves were not fully utilizing the carcasses though this varied between years.

We also discuss the other causes of caribou calf and cow mortality and the scavenging of carcasses. The presence of scavengers on a carcass is one of the factors that could have biased our finding of carcasses and we consider those factors and the applicability of our searches.

Finally, we describe our opinions on the implications of our results for the management of caribou. This section was not part of our original objective but was added at the request of CWS managers. In this section we consider the importance of a relatively disturbance-free environment on the calving ground and postcalving areas and the mother-young (maternal-filial) bond for the successful rearing of caribou calves. We discuss the implications of the relative scarcity of wolves on the Beverly calving grounds in evaluating wolf predation, and discuss wolf control as a management tool.

1. Causes of Calf Mortality

In the overall 3-year sample of 287 calves 42.9% were males, 35.9% were females and the sex of 21.2% was undeterminable. Almost all (97.6%) of those calves were estimated to be less than 1-week-old at death and most (77.0%) were less than 3 d of age.

The estimated ages of the 287 calves suggest that 3.35 calves 0-3 d old had died for every calf 4-7+ d old. Also, based on the estimated ages, we find that the proportion of 0-3 d old calves differs from the proportion of 4-7+ d old calves in the overall sample ($\chi^2 = 83.68$, 1df, $P < 0.001$). Thus, newborn calves apparently died at greater rates during the 1st 3 to 4 d of life than during the next, 3 to 4 d of life.

The calves of undiscernible sex prevented us from completely evaluating the relative proportions of females and males. However, we statistically tested the probability that the annual distributions of the sex of dead calves represented about an even sex ratio, which would suggest whether female or male calves were predisposed because of their sex to early deaths. At birth, the numbers of male compared to female calves is usually similar (i.e. about 50:50; actually, usually slightly in favour of males, Kelsall (1968:152), Skoog (1968:490), Bergerud (1969:50), Miller (1974:72). The deaths of the 287 newborn calves sampled between 1981 and 1983 were about in accordance with the expected 'secondary sex ratio' in newborn caribou. Those results indicate that neither female nor male calves were predisposed to early deaths because of their sex between 1981 and 1983.

We used counts of cows with calves at heel or cows without calves but with distended udders in June 1981-83 to evaluate overall early calf mortality (A. Gunn, unpubl. data, 1981, 1982; F.L. Miller, unpubl. data, 1983). As the counts were not taken exactly at the necessary time (taken on several days either side) for our specific purpose, the resultant values are considered only as approximations of the overall early calf mortality at about 1-week of life in each of those 3 years. We judge that a 10% total loss of calves at about 1-week or so of life in June is a good approximation for each of the 3 years of this study. All empirical impressions of early calf mortality in all 3 years during calving and early postcalving support this value. All 3 years of this study must be thought of as favourable to early calf survival in terms of prevailing weather on the calving ground and thus the results do not necessarily relate directly to years when unfavourable weather conditions might detrimentally influence early calf survival. However, we do argue that such years of extremely unfavourable weather would be relatively few over the long run when compared to years when weather did not seriously impact on newborn calves.

1.1 Stages of mortality

An extensive literature for domestic livestock and free-ranging, wild, North American ungulates deals with the internal and external factors that regulate or influence the outcome of the birth process from fertilization through parturition (see selected bibliography for examples). Quality of nutrition available to the population is the principle control over the annual rate of implantation though most all published examples are for cervids other than caribou, an exception being Thomas (1982).

The most important cause of mortality of the fetus in caribou during gestation is probably from diseases causing abortion such as brucellosis (e.g., Neiland 1965, McGowan 1966, Neiland et al. 1968, Skoog 1968, Neiland and Dukeminier 1972). Prenatal mortality is seldom of known importance in North American ungulates including caribou (e.g., Kelsall 1968, Skoog 1968, Bergerud 1971, Dauphine 1976; and selected bibliography). However, poor nutrition or abortion causing diseases could seriously reduce the actual number of calves born in any one year. Therefore, monitoring for possible prenatal loss should be an integral part of any intensive caribou management plan.

Prepartum death of the fetus and resorption, abortion, mummification, or delivery of the dead fetus would not have been detected unless the cow also had died and we found her in a condition that allowed detailed examination. We only detected in utero mortality when the dead fetus was retained (no mummified fetus was found) in the uterus of a cow that we examined or when we found a stillborn calf. Some calves diagnosed as stillborn were possibly, however, born live, but died within seconds of birth. If so, those calves would actually be an additional part to the postnatal mortality.

The level of observed prenatal mortality (fetal atelectasis - stillbirths) extrapolates to an annual rate of about 1% of the entire calf crop. This value closely agrees with the generally accepted low rates for such mortality in caribou (e.g., Bergerud 1971) and all other North American cervids (e.g., Pimlott 1959, Teer et al. 1965, Greer 1966, Hesselton and Jackson 1971). All the stillbirths appeared full term, well developed, and of viable weights (except two at 3.5 kg each). Conventionally, however, stillborn fetuses (fetal atelectasis) are considered as postnatal mortality.

The influence of the nutritional status of a pregnant cow on her calf's viability at or shortly after birth has been described for European Rangifer (Skogland 1984). Bergerud (1980:560) stated that, "The low variability in pregnancy rates in caribou on the mainland, regardless of annual difference in nutrition, is in contrast to other cervids in North America that show considerable variation (cf. Klein 1970)." Caribou are not likely different from all other North American cervids; therefore, there must be a threshold where the reduced availability of forage on winter ranges and/or the poor quality of forage on summer ranges occasionally reduces reproduction by mainland caribou. Perhaps, however, the subtle effects of restricted forage availability or poor quality are present to varying degrees and are reflected in the slight variations seen in annual reproduction within each herd. The most subtle effect would be expressed through the production of light-bodied, weak, nonviable calves that usually do not survive their first few days and certainly not their first year of life.

Predation and adverse weather have been indicated as the principle causes of death of newborn caribou (e.g., Kelsall 1968, Skoog 1968, Bergerud 1971, 1978). Under closer examination, however, the true importance of neither cause has been well documented, especially the supposed catastrophic effects of inclement weather at or about the time of calving. The prevailing weather during calving was basically favourable to calf survival for the 3 years of this study, but possibly in some years inclement weather could reasonably be considered to directly or indirectly cause significant mortality among newborn calves. Therefore, the possible importance of prevailing weather at calving time, or even during early postcalving, warrants some consideration.

1.2 The importance of adverse weather

Most work on the possible importance of inclement weather as a mortality factor of newborn caribou calves has been in Canada (Cottle 1959; McEwen 1959, 1960; Kelsall 1957, 1960, 1968; Lentz and Hart 1960; Hart et al. 1961; Pruitt 1961; Bergerud 1971; Miller and Broughton 1974). In Alaska, Skoog (1968) put forth the most information on the relationship between adverse weather and calf mortality. Many other caribou biologists both in Alaska and Canada have speculated on or mentioned this supposed relationship, most often without critically reviewing the published evidence and with at best, little supportive data other than the above literature.

Although Banfield did not directly study the subject he (1951:36, 1954:44) speculated about the effects of adverse weather on newborn caribou in Canada and concluded that, "Weather also plays an important role as a mortality factor for the caribou population. The greatest losses are suffered by newborn calves when exceptionally severe weather conditions occur during the calving season." (Banfield 1954:44). Banfield (1951, 1954) seemingly based his conclusion only on an observation of a resident of Eskimo Point, NWT, in June 1947 who estimated, "... an 80 percent calf loss in the Keewatin District herds that season." (Banfield 1954:44). The estimate was unsubstantiated by any recorded details as to how it was made. We are not saying that the observed deaths could not have been due to adverse weather, but we are questioning the reliability of the extrapolation of dead calves found around one lake to 1000s of square kilometres and the supposed magnitude of the calf loss.

Kelsall (1968; and sometimes 1957, 1960) is most frequently cited as the source of supporting data, regarding adverse weather as a major cause of mortality of newborn caribou. Kelsall

(1957:38, 1960:51, and 1968:238) when speculating about the importance of the possible deterimental impact of adverse weather at calving time suggested; "It seems likely that there is a chilling point at which the bodily functions of the caribou calf are greatly impaired. The crucial conditions are probably brought about by various combinations of wind, [humidity, (stated in 1968 only)] temperature [(not necessarily below freezing (stated in 1957 and 1960 only)] and precipitation. There is no shelter on the calving grounds except from winds, which seem to make caribou nervous and keep them on the move for greater distances and longer periods than usual. Many calves not killed outright must be separated from the herd and die later from exposure and hunger. Others must be drowned at water crossings or taken by predators. It is believed that during the calving periods in 1950 and 1951, 50 percent of the young calves may have perished in this way.". Undoubtedly, it is this general reasoning that has permeated through the then current and most all subsequent studies of calf mortality that has kept alive (in the absence of any extensive, valid, quantitative data) the belief that catastrophic mortalities of newborn caribou are caused by inclement weather at or about the time of calving.

Kelsall (1957:37-38) based his original thinking, at least partially, on a single sample of only six dead calves found after a period of "rough weather" in June 1951 and circumstantial evidence about weather conditions at or about calving in 1948 through 1951 (and likely was influenced by early Scandinavian and Russian reindeer (R. t. tarandus) literature, plus some early reindeer reports from Alaska). Kelsall did not describe cause of death of the six calves. Most importantly, this sample of only six calves is from a calving ground where tens of thousands of calves were produced in that year.

Kelsall (1960:51) parlays the small sample of six dead calves from June 1951 into, "...considerable mortality among young calf caribou, which they ascribed, directly or indirectly, to adverse weather.". Kelsall (1960:51) continues his speculation by noting that finding 30 intact skeletons of young calves in spring 1954 that apparently had died in spring 1953 did not implicate wolves but "...might be correlated with blizzard conditions which had prevailed in 1953 during the height of calving.". We suggest that predation, pathological conditions, or other physiological disorders could also just as likely have been implicated as could adverse weather.

Kelsall (1960:45-50) continued his speculation about the direct and indirect importance of adverse weather on newborn caribou: using a sample of only four of nine dead calves found in June 1957 and 30 dead calves (35% of 85) found in June 1958 and circumstantial evidence from weather records and counts of cows with calves. Kelsall (1960:45) again gave no postmortem examination results to support the diagnoses or to identify the actual causes of death. Kelsall (1960:46) further speculates about the possible indirect importance of inclement weather in causing increased mortality of newborn calves, "Injuries would be more likely during blizzards. At such times separation of the calves from the cow would inevitably be more frequent, predators would find hunting easier, and calves with inherent weaknesses would be less likely to survive their first few days.".

Kelsall's (1960:45) reporting of a sample of only nine calves in June 1957 is confusing in light of Kelsall and Loughrey's (1958:27) observations during the calving period of 1957 of, "Fifteen caribou evidently killed or eaten by wolves were found, including five adults, one yearling, and nine calves.". It seems that the 1957 calf sample should have been at least 18: 11 suspect wolf kills; 4 deaths supposedly due to adverse weather (exposure or starvation); and 3 unknowns. If this is true, it would create further doubt about the justification for the speculation about the supposed relative importance of adverse weather, at least, when based on direct evidence from samples of dead calves.

We do not necessarily disagree with the above reasoning but we do question the inferred magnitude of the supposed mortality. We suggest that (1) injuries and separation might be more prevalent during blizzards but it is unlikely that migratory barren-ground caribou have not evolved behavioural patterns under such conditions to the extent that would, at least, prevent such events from regularly occurring at catastrophic or at lower but still significant levels. If caribou have not evolved such behavioural patterns to cope with such events, it seems, that the alternative must be that they do not routinely experience severe enough combinations of inclement weather at or about the time of calving to have been forced to do so (which is seemingly most likely the case for, at least, Newfoundland; Alaska; and, at least, parts of the Old World range).

Kelsall (1960:56) states, "More than 100 dead calves found appeared to have died during the adverse weather of June 1 to 3 and June 5 to 10." [1958]. He further states (p. 56) that, "At Camp 26, where Wilk, Thomas and Pruitt discovered about 90 dead calves, most of the mortality had occurred during the first ten days of June.", seemingly, implying that it was caused by the adverse weather noted above between 1 and 10 June. Kelsall (1960:45) had previously stated that in total only, "... more than 100 dead young calves were found.", at all three camps. Those carcasses were found until 26 June but, "... most of them were thought to have died during the adverse weather experienced up until June 11." The causes of death were discussed for only 85 of them (which he refers to as, "... about 90 dead calves," on p. 56) and only 35 percent of them (30) were attributed directly to adverse weather (p. 45). It seems that Kelsall had distorted his sample sizes and the relative importance of adverse weather in his discussion (p. 56). Also, it is difficult to adequately determine the "time of death", except when the carcass is relatively fresh or more grossly when the carcass is relatively very old (and only then, if detailed necropsies were performed - which is never specified). Kelsall (1960:48) only mentions the skinning of five carcasses by de Vos and not any detailed postmortem examinations.

The field workers apparently determined the supposed cause of death merely by finding the carcasses after periods of inclement weather and not finding any external evidence for each calf's death by other causes. Our study of calf mortality on the Beverly calving ground and studies on the calving ground of the Porcupine caribou herd in Alaska (Mauer et al. 1983, Whitten et al. 1984) emphasizes the need for detailed postmortem internal examinations to determine the cause of death. Determination of exposure as a cause of death from only an external examination of a carcass is essentially impossible, and even after performing a detailed necropsy would often still be questionable, as such a determination is made by the process of eliminating other causes.

de Vos (1960) is often cited in relation to adverse weather contributing to deaths of newborn caribou but his only relevant statement was, "In this particular study inclement weather did not appear to affect calf mortality seriously. On June 12, four dead calves were found which appeared to have succumbed during a blizzard three days previously." This situation is puzzling as de Vos' camp was one of the three camps of Kelsall (1960) that supposedly provided data on the importance of adverse weather in 1958, especially as it was located only about 5 km from the camp where the 85 carcasses were found (D.C. Thomas, pers. commun.; and map no. 2 of Kelsall 1960:137).

Also relevant is Pruitt's (1961) findings referred to by Kelsall (1960:48) that suggested that only, "... about 4.5 percent (or possibly less)..." of the calves observed during 6-9 June 1958 died during that period of adverse weather. Pruitt's (1961:551) subsequent conclusions have been unheeded (1) "It is clear that near-blizzard conditions prevailed during most of the period of observation." - (yet mortality was very low!); and (2) these results, "... serves to emphasize the possible physiological differences between domestic reindeer and wild caribou, in addition to the behavioural differences..." (Pruitt 1960).

Altmann (1962:16) stated that, "It is enigmatic that caribou are born well before the warmest time of the year on the barren grounds, and yet, may be highly susceptible to incliment [sic] weather.". He suggested that one possible explanation was that if caribou were born earlier the influence of adverse weather would be more likely and if born later they would not make sufficient growth to survive the first winter. Other environmental trade-offs are implicated and of particular importance to late born calves would be the hordes of blood sucking and biting insects that occur by July of each year that would interfer with mother-young bonding and nursing behaviour.

Kelsall (1968:236-242) in his final consideration of weather (especially wind chill) in relation to newborn calf mortality basically reiterated his previous reports and reports by Lentz and Hart (1960) and Hart et al. (1961). Only additional data for June 1959 field work are included, and no samples of dead calves were obtained in that year. Kelsall's (1968:239) statement that, "Numerous dead calves were found following severe storms in all three of the later years, (1957-59) with losses in 1959 being relatively minor, and those in 1957 quite severe." is misleading. The deaths of four of nine calves in June 1957; 30 of 85 calves in June 1958; and none in hand in June 1959 do not translate to "Numerous dead calves...". Also, we think, that Kelsall's circumstantial evidence from weather records and counts of cow-calf ratios obtained in the above studies do not necessarily support the conclusion that mortalities of newborn calves in those years must be attributed directly to adverse weather.

Kelsall's (1957) concerns for severe weather leading to the death of calves led to experiments to describe the influence of adverse weather on metabolic and thermal responses of newborn caribou (Hart et al. 1961, Kelsall 1968:238-240). Extrapolating Hart et al.'s (1961) study to healthy, free-ranging calves is questionable: the experimental calves were (1) captured and flown to holding areas; (2) held in small corrals, without forage, and fed a substitute diet of mainly evaporated milk; (3) tethered by a rope during tests; (4) some were blindfolded to prevent struggling during tests; and (5) tested while in the standing postion. Only four of the calves tested died apparently of direct results caused by adverse weather. Those four calves were tested during a heavy rain storm on 15 June 1959: two died during the tests; and two subsequently succumbed after testing was completed. Most importantly, however, is that four untested (control) calves free to find shelter around the camp during the storm all survived. Hart et al. (1961:855) recognized the probable importance of behaviour when they concluded, "Certainly the survival of many species in a seemingly adverse environment can be attributed, at least in part, to their avoidance of the extreme conditions presented." Additionally, they noted that the effect of the storm during the test period could not be detected by subsequent repeated counts of cows with calves. Thus suggesting that, at least most all, free-ranging calves were able to cope, in some manner, with the adverse weather conditions that led to the deaths of the four restrained, test calves. The restraint of the four test calves probably psychologically and physiologically stressed them additional to the physiological stress of the storm which further dimishes the direct application of the experiment (especially at the level of the threshold values obtained) to free-ranging calves.

Cottle (1959:10) when discussing the 1959 wind chill study also made the same supposition, "The apparent survival [referring to subsequent counts with ratios of as high as 94 calves per 100 cows, indicating that the effect of the storm was not evident] of young animals in the wild suggests that behavioural patterns of both young and the female adult are important factors in the survival of the young during adverse conditions.". Additionally, on 16 June 1959 McEwen (1959:37) saw 20 dead calves from the air, following an exceptionally severe storm on 15 June with rain and winds of 80 km/h gusting to 121 km/h. He (McEwen 1959:37) extrapolated the 20 dead calves seen on a 86 km^2 area to 533 dead calves on a supposed calving ground of 2779 km^2 and estimated a 2.6% mortality on 15 June (by assuming 19 800 calves present). When he compared this loss to earlier losses he (McEwen 1959:37) concluded, "Although this is perhaps not a valid comparison, it does indicate that the effect of weather on calf mortality was lower than anticipated."

In 1960 McEwen (1960:27) concluded that calf survival was high because of favourable weather throughout the calving period, with the exception of one day. He implied that the sighting of seven dead calves on 9 June, a "... slightly higher than daily average." (McEwen 1960:27) resulted from inclement weather on 8 June with 9.0 mm of rain and winds averaging 32 km/h.

Bergerud (1971) who worked on woodland caribou in Newfoundland (R. t. terraenovae; R. t. caribou, Banfield 1961) concluded that there was no evidence that calves succumbed from exposure between 1957 and 1967. He reported that of six calving grounds the one with the coldest weather had the second highest 10-yr average rate (15.2%) of calf survival (Bergerud 1971). However, Bergerud (1971) also pointed out that the maximum daily wind chill values for June in those 11 years were less than those given by Kelsall (1960) and Hart et al. (1961) as causing mortality of newborn caribou calves in the NWT. He also suggested, and we concur, that as newborn Newfoundland caribou calves are heavier than barren-ground caribou calves the former might be able to withstand greater exposure to inclement weather (Bergerud 1971).

However, when discussing North American caribou in general, Bergerud (1978:86) states that, "Wind chill is the second most common cause of death of newborn calves during inclement weather (cf. Kelsall 1968)." "...(and) this cause of mortality can deplete an entire calf crop.". The above unsupported statement is then followed by an erroneous citation, "The Kaminuriak herd lost much of its 1962 calf crop from this factor (Miller 1974).". Miller (1974:65-66) only concluded that, "..., we must assume that either the survival of calf crop in 1962 was very low, or the mortality of juveniles and subadults of that cohort was exceedingly high." Miller (1974) drew no conclusions about the possible importance of wind chill in directly causing or indirectly contributing to mortality of newborn calves in 1962. Data indicating record snow depths on the winter range (Parker 1972:Table 5) and observations of caribou in extremely poor physical condition during spring migration in 1962 (J.D. Robertson, pers. commun. in Miller 1974:66) argue for the causes of calf mortality having been initiated well in advance of calving. Observations by Ruttan (1962) in August 1962 also suggested that the calf crop was either low or suffered high early mortality. Inclement weather at the time of calving as a possible significant contributing factor in the death of calves in 1962 cannot be ruled out, but no evidence for it exists either.

Bergerud (1980:560) subsequently correctly evaluated the problem of prevailing weather on the Kaminuriak calving ground in June 1962, when he stated that, "We do not know the severity of the weather on the calving grounds in 1962.". Bergerud concluded (1974b:557) that, "The short calving season for caribou cannot be explained by a mortality due to weather of calves born too early in spring. Calf mortality due to windchill has been reported for the Canadian Arctic

(Kelsall, 1968) but not for Alaska or Newfoundland (Lent, 1964; Skoog, 1968; and Bergerud 1971)."

Skoog (1968:581-587) found no evidence for adverse weather at or about calving time causing significant losses of newborn caribou in Alaska. He accepted, however, the supposed importance of adverse weather in causing high mortality among newborn calves, and concluded (Skoog 1968:582-583) "There can be no doubt that severe weather and chilling can result in high mortality among new-born calves during some years.". He referred to turn-of-the-century reports of high losses within calf crops of reindeer (Skoog 1968:581-582) and the later Canadian reports (Banfield 1954, Kelsall 1957, Lentz and Hart 1960) for supposedly supportive data. But then Skoog (1968:583) seemingly implied that the relative early calving by reindeer in Alaska probably accounted for high losses of newborn calves during adverse weather; further stating that, "Caribou have the advantage of dropping their calves at least a month later in Alaska, and in northern Canada, a month and a half.". Skoog (1968:587) summarized his discussion about weather by saying, "I doubt, however, that weather conditions other than icing exert much influence over caribou populations, except occasionally when repeated losses of a majority of a calf crop may occur over a period of years. The Nelchina herd experienced no such losses during the period of this study.".

Again, seemingly, theoretically sound reasoning but no quantitative data not even any circumstantial evidence to support the likelihood of such losses. Reliance on reindeer literature and uncritical evaluations of the Canadian literature perpetuated the supposed importance in Alaska of adverse weather at or about calving in causing high mortality among newborn caribou. No subsequent studies of caribou calf mortality in Alaska have to date documented any such high losses (and for the most part, not even any insignificant losses) of newborn caribou calves due to adverse weather (Bos 1973, 1974, 1975; Davis and Preston 1980; Davis et al 1978; Davis and Valkenberg 1978, 1979, 1981; Mauer et al. 1983; Whitten et al. 1984).

Davis et al. (1978) found no calves that had died from exposure to adverse weather in a study of the Fortymile caribou herd in Alaska. While discussing the possible losses of calves to adverse weather they noted (Davis et al. 1978:60), "Caribou investigators in Alaska have pointed out that conditions on Alaskan calving grounds are generally milder than those in northern Canada.". They further noted (Davis et al. 1978:62) that, "It is interesting to note that the Delta caribou herd (the closest neighboring herd to the Fortymile) realized its highest recent initial calf production and survival during 1972. Department biologists surveyed that area because they were concerned that catastrophic calf loss might result from the low temperatures and heavy snowfall in spring 1976. We also documented highly successful calving in the Western Arctic herd in 1975 and 1976 under weather conditions that were harsher than those that occurred on the Fortymile calving grounds during this study.".

Although much of the speculation about the importance of adverse weather at or about the time of calving in causing significant levels (let alone catastrophic ones) of mortality of newborn caribou appears reasonable, virtually no quantitative data exist to support the supposed magnitude or the frequency of occurrence of the problem.

The speculation is based on limited, quantitative data and is suspect because actual cause of death was not determined by detailed post-mortem examinations; data were not clearly presented; and some findings were distorted in the literature.

The physiological experiments are questionable, especially the meaningfulness of the threshold values, because restraint or only parts of the animal were used and because behavioural considerations (avoidance of extremes) were ignored in drawing conclusions.

We think that Bergerud (1980:560) hit on the crux of the matter regarding the probable importance of adverse weather at or about the time of calving (especially at the peak of calving) when he stated that, "We do not clearly understand the relationships between maternal nutrition, calf size and vigor, and the subsequent ability of the calf to survive severe weather.".

The circumstantial evidence associated with Kelsall's meagre samples of dead calves does not necessarily support the assumptions that the mortality had to be weather related, or that such high losses due to adverse weather are common events. Some other undiscerned cause(s) of mortality could have been operative, or high losses due to adverse weather could have been infrequent and sporadic. Healthy newborn barren-ground caribou are well adapted physiologically and behaviourally to cope with all but the most extreme severities of adverse weather at or about the time of calving. Significantly high mortality among newborn barren-ground caribou probably only occurs when the additive effects of several unfavourable conditions combine: e.g., forage unavailability lowers the nutritional status of pregnant cows to the extent that their calves are light, weak calves.

1.3 Wolf predation

Wolf predation was the most important cause of mortality to newborn caribou calves during their first week of life on the Beverly calving ground in June 1981, 1982 and 1983 (Tables 3 and 4). Possibly, wolves killed about 5-7% (50-70% wolf kills x 10% early calf mortality) of the calf crop in June of those years. This is based on the assumptions that the contributions of wolf-killed calves to the three annual samples of dead calves are representative of the relative importance of wolf predation and that about 10% of the calf crop had died by 1-week of age in June of those 3 years.

On the basis of our samples of wolf-killed calves in all 3 years, only a minor portion (12.8%) are likely to have been predisposed to death by wolf predation because of physiological or pathological disorders. Compensatory mortality is a minor consideration in the evaluation of the impact of wolf predation on newborn caribou calves during calving and early postcalving of the Beverly herd. We must assume that most calves (at least 87.2%) <2 weeks old that were killed by wolves would have otherwise survived.

Between 1981 and 1983 the 19 calves classified as suspected wolf predation were only 7.4% of the 257 calves that had causes of death assigned to them. In 1981 the 14 cases of suspected wolf predation increased the wolf-kill of 23 calves by 37.8% to an apparent 37 calves. This contribution would markedly increase the overall importance of wolf predation on newborn calves by 20.0% in 1981. In 1982 and 1983 the increases from the two and three cases of suspected wolf predation only slightly increased the wolf-kill of 69 and 62 calves by 2.8% and 4.6% to an apparent 71 and 65 calves. These contributions would cause only minor increases in the overall importance of wolf predation on newborn calves: 2.2% in 1982, and 3.1% in 1983.

Many authors have argued about the importance of wolf predation on newborn caribou calves, but their evidence was only meagre samples of wolf-killed calves, if any (e.g., Murie 1935, Clarke 1940; Murie 1944; Banfield 1954; Harper 1955; Crisler 1956; Kelsall 1957, 1960, 1968; Pruitt 1960; Skoog 1968; Bergerud 1971, 1974a, 1974b, 1978, 1980; Clark 1971, Kuyt 1972; Parker 1972; Miller 1974, 1982, 1983; Miller and Broughton 1974; Bos 1975; Cumming 1975; Curatolo 1975; Miller 1975; Davis et al. 1978; Davis and Valkenburg 1978, 1979, 1981; Davis and Preston 1980; Boertje 1981; Fleck and Gunn 1982; Gasaway et al. 1983). Those reports of calf mortality due to predation cannot be directly compared to this study, because those studies include neonatal mortality of caribou over several weeks or months. Only few data are reported on calves estimated to be 2 weeks or less of age.

The sex and age distributions of the wolf-killed calves in each year indicate, to varying degrees, that (1) wolves did not select newborn calves (<1 d) and (2) there was apparently selection for younger (<4 d) rather than older (≥4 d) calves. However, regardless of this apparent selection by age, calves remained vulnerable throughout their first week of life.

The 1970 Kaminuriak calf mortality study (Miller and Broughton 1974) is comparable with our results based on 31 calves estimated to have been ≤7 d old or on 43 calves ≤14 d of age. On this basis the wolf predation on the Kaminuriak calving ground in June 1970 amounted to 19.4% (6/31) for calves ≤7 d old and 25.6% (11/43) for calves ≤14 d old (overall wolf predation during calving and early postcalving was 31.6% (18/57) for calves ≤7 weeks old). The percentages of newborn calf mortality attributed to wolf predation on the Kaminuriak calving ground in 1970 were lower than those found in each year of this study on the Beverly calving ground. However, more wolf sightings (n = 19) were made in June 1970 on the Kaminuriak calving ground than were made on the Beverly calving ground during any of the 3 years of this study. The rates of wolf predation on calving grounds do not seem to necessarily reflect the number of wolves actually seen.

As in this study, wolves on the Kaminuriak calving ground in 1970 appeared to show a preference for eating milk curds, then viscera, and finally flesh. It appeared that wolves deliberately took stomachs and ate the milk curds, based on examinations of carcasses of wolf-killed calves in 1970 with only part of the viscera missing (Miller and Broughton 1974, Miller 1983).

Kelsall (1968:242-260), Skoog (1968:611-619), and Davis *et al*. (1978:29-60) have reviewed predation on caribou in detail. The food habits of wolves involving caribou have been discussed in various detail: e.g., Clarke (1940), Murie (1944), Banfield (1954), Harper (1955), Burkholder (1959), Kelsall (1968), Rausch (1968), Skoog (1968), Clark (1971), Kuyt (1972), Miller and Broughton (1974), Bos (1975), Curatolo (1975), Miller (1975), Stephenson (1975), etc. As noted by Davis *et al*., (1978:35) "a complete picture of wolf food habits is presented in Mech (1970) and Stephenson (1978)."

Essentially all studies in North America considering wolves and caribou calves have offered the same two general conclusions: (1) wolves are important predators of newborn calves; and (2) wolf predation (and predation by all other predators) is most severe in the first week or two of the calf's life. For example: (1) Murie (1944) reported that wolves kill caribou calves that are only a few days old with little effort. (2) Kelsall (1968) thought that only the "very young" caribou calves would routinely fall victims to wolves. (3) Skoog (1968) found that caribou calves are especially vulnerable to wolf attack and that those <2 weeks of age had little chance of escaping.

Managers and biologists seemingly accept that predation is most often an important cause of mortality of newborn caribou in North America. The important variables are which predators are involved and the magnitude of the predation on a herd basis. For the Beverly herd the wolf is the principle predator and appears (at least in the 3 years of this study) to be annually responsible for at least one-half of the early calf mortality. Findings from Heard and Decker (1980), seemingly, add further support to our conclusion regarding the importance of wolf predation as a cause of early calf mortality in the Beverly herd. Wolf predation is an omnipresent factor of mortality for caribou (Skoog 1968:661, Bergerud 1978:87) and this is especially true for the migratory barren-ground caribou of the Beverly herd.

1.3.1 Multiple killings by wolves

Direct evidence for the rates and efficiency of killing newborn calves by wolves was obtained during the 1981-82 study of cow-calf behaviour on the Beverly calving ground. K. Jingfors and R. Mulders were fortunate to observe twice multiple killings of newborn calves by single wolves that demonstrate the ease by which wolves can catch and kill neonate calves.

Observation of 19 June 1981

1810 - A lone wolf was observed chasing a group of 200-300 caribou. The wolf singled out a calf and chased the zigzagging calf for about 10 seconds. The calf went down, but it was impossible to determine how it was killed. The wolf stopped and stood briefly along side the downed calf before carrying it to a snowbank; where it dug a hole and cached the calf under the snow. It then used its nose to push the snow back over the calf.

1815 - The wolf again chased the caribou group. It singled out another calf and was running about 10-15 m behind it. The other caribou dispersed in clumps. Both wolf and calf disappeared out of sight behind a ridge.

1830 - The same wolf reappeared and chased a calf along a ridge. The wolf ran easily with its tail straight up. The wolf grabbed and killed the calf (killing bite missed), picked it up, circled, put the calf down, and then walked about 25 m onto a snowbank and bedded.

1833 - The wolf rose and trotted past the dead calf and disappeared over a ridge.

1834 - The wolf reappeared, chased and easily overtook and killed a fourth calf (killing bite missed). The wolf picked up the calf and carried it along the ridge, disappearing from view at 1836.

The carcass of the first calf was the only one that could subsequently be located by the observers. The calf was a male, estimated 4-7 d old, and weighed 9.0 kg. The carcass was intact and externally no wounds were visible. Once skinned and the body cavities opened, the carcass revealed canine tooth punctures in the upper portion of the rib cage and spinal area, tissues of the right rib cage and right femur were severely tramatized, and there were canine tooth punctures in the tip of the right diaphragmatic lobe of the lungs, resulting in profuse hemorrhaging in the thoracic cavity. All other evidence indicated the calf was generally healthy and well nourished.

Observation of 17 June 1982

1052 - Several hundred caribou became alerted and started galloping from a wolf that walked into sight. The wolf loped after the caribou, stopped and squatted on a hummock, then continued at a steady lope after the caribou.

1054 - Amidst the confusion following its appearance, the wolf easily caught its first calf. The wolf briefly ran and caught the calf by the rump. The calf fell, apparently dead (killing bite apparently missed by observers), and the wolf continued without hesitating. However, it may have bitten the calf in the head as it passed by. In less than 30 seconds the wolf caught up with another calf and appeared to grab it by the rump. The calf went down and the wolf bit the calf's head before running after more caribou.

1055 - The wolf left its second kill, about 75 m from the first kill, and ran upslope after a third calf. Within about 15 seconds the wolf caught the calf apparently by the rump. The calf went down, but its ears continued to move. The wolf stopped and picked it up (seemingly, bitting it in the head as it did so), then laid it on its side.

1056 - The wolf was standing over the third kill, facing to the south. A small group of about six caribou were seen moving to the west and the wolf ran toward them.

1057 - The wolf went out of sight behind a ridge as it chased a cow.

The above observations confirm that single wolves are able to kill newborn calves easily and at high rates. In 6 min of hunting activity on 17 June 1982 the single wolf killed three calves. The actual time between the first and third kills was, however, only 3 min (1 calf/min). On 19 June 1981, the single wolf took at least three calves, we believe four, during 28 min of hunting activity: the actual time lapsed between the first and observed third kill was 24 min (1 calf/8 min) or between the first and supposed fourth kill (1 calf/6 min). Any application of these rates to the daily hunting and killing activities of single wolves would predict kills in excess of the wolf's need for short-term sustenance. A single wolf does not need more than one caribou calf per day to meet its maintenance requirements (Mech 1970, Kuyt 1972).

Perhaps, the best documented example of how quickly a wolf responds to an opportunity to kill caribou calves is given by Dauphine (1969:99). On 10 July 1967, while travelling by canoe on the Thelon River west of Aberdeen Lake, Dauphine disturbed a wolf on the shore. The wolf took flight and ran away paralleling the shore; a caribou calf jumped up about 10 m in front of the wolf and ran perpendicular to the wolf's course of flight; the wolf instantly swerved, overtook the calf, knocked it down, and seized it by the back of the head. The wolf then shook the calf violently, killed it, dropped it, and then continued running away without further hesitation, disappearing over a hill about 170 m away. Although the wolf was in the process of fleeing the human-caused disturbance; the sudden presentation of a prey target at close range, caused the wolf's predatory drives to override its escape behaviour. Thus, delaying its escape long enough to make the kill; obviously, with no intentions of utilizing the kill. Such behaviour argues strongly for the likelihood of high rates of predation being common on the calving ground, when easily caught and killed prey, newborn caribou, are abundant.

1.3.2 Surplus and/or excessive killing by wolves

Our finding of 34 calves all killed within a short time period of each other on a 3 km^2 area is our best example of "surplus killing" of newborn caribou by wolves (see Section 4.1.1). Most likely our findings of 68.8% (106) of all wolf-killed calves in clumped associations, usually with little or no carcass utilization by wolves, is further supportive evidence of excessive killing of newborn calves by wolves.

Kruuk (1972:234) defined surplus killing ..."as the killing by a predator of prey, without the killing individual or its offspring or members of the same social unit eating anything from the kill, although there is free access to the carcass and usually the particular prey species would be eaten by that predator." Kruuk's definition implies there are three conditions that have to be met for predation to be considered an example of surplus killing. These three conditions are that (1) the carcass is not immediately consumed by the predator or its offspring or social unit members; (2) the predator has free access to the carcass, and (3) the prey species is normally taken by the predator.

Wolves did not consume any parts of 17 of the 34 calf carcasses found on the 3 km^2 area. We cannot fully differentiate predator feeding from scavenging in all cases, so we could not exclude the possibility that the wolves, (or their offspring or pack members) which killed the remaining 17 calves consumed parts of them. If they did consume parts of the remaining 17 calves, according to Kruuk's (1972) definition, then only the first 17 of the 34 carcasses would be regarded as surplus kills. Kruuk (1972) did not strictly adhere to his own definition in his examples of surplus killing, as some of the prey in his examples were partially consumed. We suggest that Kruuk's (1972) definition be modified to include consumption of some of the prey. To specify a proportion would be meaningless because of the large variation among different situations.

An obvious argument against surplus killing is that the wolves would have returned to consume all the kills but were prevented from so doing by the removal of the carcasses by us. Kruuk's second implied condition for surplus killing is that the predator had free access to the carcass but he did not imply whether there was a time limit in which the predator should return. The 34 dead calves that we found probably had been dead for about 24 h and apparently the wolves had not yet returned and fed on them. Gulls can strip a calf carcass of viscera and the main muscle masses in less than 48 h (unpubl. data). Therefore, our removal of the carcasses shortly preceded their being scavenged by gulls, which would have made them unavailable to wolves, and probably did not influence the return of the wolves.

The third condition, that the prey be a usual prey species of the predator, is fulfilled as barren-ground caribou are the usual prey of wolves in the study area.

The failure of the predator or a group of predators to consume all prey killed within brief time intervals can be caused by several conditions. Kruuk (1972) discusses the relevance of food caching as it relates to surplus killing. If, however, surplus killing is explained as food caching, it seems surprising that at least in the case of the 34 calves no efforts were made to conceal the carcasses in the snow banks or gravel in the area which would have been necessary to at least retard the depredations of scavengers. Only one wolf was seen to nose snow over a freshly killed calf during the observations of wolves killing caribou calves on the Beverly calving ground without utilizing the kill.

Specialization in hunting roles within a social unit, with some predators in a social unit hunting for other members, was suggested by Kruuk (1972) as a behavioral pattern that could break down and lead to surplus killing if numerous prey were available. Wolves on the Beverly calving ground most often occurred as pairs or singles and most likely hunted for themselves. Thus, social hunting is not applicable as each wolf apparently hunts for its own prey.

Mysterud (1980) described extreme specialization in food selection as being one response to increasing prey densities, and suggested that high prey densities could lead to surplus killing. Extreme food selection has been described by Mysterud (1980) in European brown bears which apparently learned to consume only the udders and sternal fat tissue from domestic sheep (*Ovis aries*). The selection of udders is particularly interesting, because all calves in our study that were fed on by predators had their stomachs removed. No milk curds were left in or near the carcasses. Subsequent scavenging, however, prevents us from positively determining whether the milk curds were removed by the wolves or the gulls. As half of the 34 calf carcasses were not fed on by wolves, and only certain parts were removed from the remainder, our observations represent surplus killing as well as food selection.

The environmental conditions that led to other reported instances of surplus killing were absent in the example we are reporting. Surplus killing has been reported for (1) wolves killing caribou under deep snow conditions (Eide and Ballard 1982); (2) wolves killing reindeer during a heavy snowstorm (Bjarvall and Nilsson 1976); (3) wolves killing white-tailed deer in deep snow (Mech *et al*. 1971); (4) black bears (*Ursus americanus*) killing restrained and free-ranging domestic stock (Kruuk 1972, Horstman and Gunson 1982); and (5) hyaenas (*Crocuta* spp.) killing Thomson's gazelles (*Gazella thomsonii*) during dark and stormy nights (Kruuk 1972). Estes and Estes (1979) suggested that malnutrition of wildebeest calves (*Connochaetus taurinus*) may have contributed to surplus killing by hyaenas described by Kruuk (1972). The intact caribou calves that we examined were in good physical condition with traces of kidney fat and viable body weights. Unusual environmental conditions that would facilitate surplus killing were absent on the Beverly caribou calving grounds in 1981-83.

Miller and Broughton (1974:10-11) concluded that much, if not all, of the excessive killing of newborn calves by wolves was restricted to young, nonbreeding wolves which are motivated by drives associated with learning in young predatory animals; that is by the need for practice and play. Miller (1974:63) expanded this supposition to include the belief that adult wolves are usually governed more by restrictive consumatory drives and the need to conserve energy. It now seems more likely, however, that the sheer abundance of easily caught and killed prey at or about calving time on the caribou calving grounds allows all wolves present regardless of age or sex to kill in excess of their short-term need for sustenance.

R.O. Peterson (pers. commun.) pointed out that wolves probably have no inhibition against killing vulnerable prey. In the rare case (rare from the individual's standpoint) when a wolf is faced with abundant, vulnerable prey, there does not seem to be an adaptive reason why a wolf would not kill as many prey as possible, unless there is a danger of injury during the killing.

In June 1978, 28 dead caribou calves were examined on the Beverly calving ground by D.C. Heard and R. Decker (pers. commun.). They found that 61% (17) of the calves had been killed by wolves and that only 29% (5) of them had subsequently been fed on by wolves. Heard and Decker (pers. commun.) believed that strong winds, snow, and low temperatures that prevailed between 5 and 8 June 1978 predisposed these calves to wolf predation. Six of the wolf-killed calves were found within about 150 m of each other on 12 June and none had been fed on by wolves (D.C. Heard, pers. commun.). Although those calves were not reported as surplus killing they fit the category. The other 11 wolf-killed calves were found as singles: 3 found on 13 June, 5 on 15 June, and 3 on 29 June (D.C. Heard, pers. commun.).

The four published reports of apparent surplus killing by wolves of caribou or reindeer are not as clear as our findings. Miller and Broughton (1974) reported apparent surplus killing of caribou calves by wolves. Utilization of wolf-killed calves in the Kaminuriak study also varied greatly (Miller and Broughton 1974). In 1970 carcass utilization for the six wolf-killed calves <7 d old ranged from none to 90%: one calf was untouched after being killed; one had only part of the viscera removed; two had all viscera removed; one had all the viscera and muscle tissue from the right hindquarter taken (estimated 45% utilized); and one had all but the lower portions of the four legs missing (esimated 90% utilized). Carcass utilization in 1970 for the five wolf-killed calves >7 d old and ≤14 d old ranged from slight to 80%: one had only part of the viscera taken; two had all the viscera removed; one had all the viscera and some muscle tissue removed from its hindquarters and along the back (estimated 50% utilized); and one had all but the head and lower portions of the legs taken (estimated 80% utilized). Carcass utilization in 1970 for the seven wolf-killed calves >15 d old ranged from none to only 35%: five were untouched after killing; and one had all of the viscera and some muscle tissue gone from both sides of the withers and the left shoulder. Crisler (1956) observed a wolf kill two calves and fatally wound two others in 0.5 h in a postcalving aggregation. Murie (1944) working in Mt. McKinley, Alaska, found three uneaten calves that had been killed by wolves in a small area. Eide and Ballard (1982) found seven wolf-killed caribou carcasses on 31 March 1979 in a 3 km^2 land area (1-km radius): the carcasses were scavenged so the degree of use by wolves was unknown. Bjarvall and Nilsson (1976) recorded two wolves killing 40 reindeer in 2 weeks with eight being killed during one night. They did not report whether the wolves fed on the carcasses or the size of the land area in which the kills occurred.

We believe that identification of surplus killing should be restricted to cases where the prey items are found in a clumped distribution with, at least, some of the individual prey items never having been fed on after being killed. Perhaps, it would be best to restrict the term "surplus killing" to only cases where absolutely no use is made of the kill by the killers or their family or group members; and term cases of low rates of use "excessive killing", as suggested by Carbyn (1983). We do not think that cases that involve some utilization of the carcasses even though only at low rates should be termed surplus killing.

In most years, few wolves are observed on the Beverly calving ground during calving and early postcalving (Fleck and Gunn 1982). For example, only 10 sightings of wolves were made during 316 h of systematic ground observation time by six observers, several hundred hours of incidental observational time by nine field personnel, and about 125 h of helicopter flights over the Beverly calving ground between 3 June and 2 July 1982. In comparison, we made 100 sightings of wolves in only about 70 h of helicopter flights over Beverly caribou herd winter range between 18 March and 12 April 1983 (unpubl. data). Our observations of the ease with which wolves can kill calves, while sometimes making little use of them suggest that even the low numbers of wolves on the calving ground may cause significant mortality.

1.4 Grizzly bear predation

The state of the carcasses of two apparent grizzly bear-killed calves in 3 years does not rule out the possibility that the calves were not killed by grizzly bears but were scavenged by them. Calves killed or scavenged by grizzly bears likely would be completely utilized so that only fragmentary remains would be found. The bear's habit of scraping vegetation and soil over its kills would reduce the conspicuousness of the kills and possibly we missed seeing such kills. No comparisons can be made among years and no objective assumptions can be made or conclusions drawn about the utilization of calf carcasses by grizzly bears.

Four possibilities are suggested by the presence of some placental tissues on the pelages of the two calves which were possible grizzly bear kills (each of these two calves was found next to the carcass of its grizzly bear-killed maternal cow). (1) The 'calf' was a full term fetus pulled from the cow by the bear after it killed the cow. (2) The cow was actually calving when killed by the bear and the fetus was partially or fully delivered. (3) The calf was stillborn or died of some patho-physiological disorder, and the cow was standing over its dead neonate when killed by the bear. (4) The calf was healthy and was killed by the bear.

We do not know what caused the among year variation in grizzly bear occurrence on the Beverly calving ground between 1981 and 1983. Perhaps, the lateness of the 1982 spring (no bears seen) compared to the relatively early springs in 1981 and 1983 influenced the distribution of grizzly bears. Grizzly bears might occupy the more northerly areas of their ranges in June in years with relatively more snow free ground. In years with heavier snow cover and less snow free ground, such as 1982, bears remain along the Thelon River system to the south, where the snow retreats before it does on the calving grounds north of the Thelon.

The lack of grizzly bears on the calving ground during calving and early postcalving in 1982 suggests bears do not annually seek out newborn caribou as prey nor do those bears respond to the relative abundance of carrion from dead caribou on the calving ground. Possibly, the food supply is too temporary to exploit or there are sufficiently adequate food supplies to hold the bears elsewhere.

Several studies in Alaska have identified the grizzly bear as an important predator of newborn caribou (e.g., Lent 1960, Skoog 1968, Reynolds 1980, Davis and Valkenburg 1981, Mauer et al. 1983, Whitten et al. 1984); and one study on woodland caribou in British Columbia (Bergerud 1979). However, sightings of grizzly bears on calving grounds in the NWT have been consistently low over the years (Fleck and Gunn 1982:Table 15; and Table 37, this study). There has been (Kelsall 1960) and there appears to still be (Cooper 1981) a relatively large reservoir of grizzly bears along the Thelon River system west of Beverly Lake and south of the current (1981-83) Beverly calving grounds. When and if numbers of grizzly bears increase on the Beverly calving ground, some bears will likely learn to actively seek out and hunt both newborn calves and adult female caribou. If this occurs, the importance of grizzly bear predation could increase.

The potential for this condition occurring seems real as it could happen either through bears expanding their May-June range northward or the Beverly caribou reverting to previously used more southerly calving areas (Fleck and Gunn 1982). This possibility suggests that more effort should be made to record by date the numbers and locations (by lat./long.) of grizzly bears seen on the Beverly calving ground at or about calving time (this need for better records applies to sightings of wolves and all other potential predators of newborn calves). It is impossible to determine from current records the actual location of reported sightings of most wolves or grizzly bears relative to the actual calving ground used in that year.

1.5 Atelectasis

We found 45 cases of atelectasis: (1) 14 cases of fetal atelectasis (10 males and four females); (2) 18 cases of neonatal atelectasis (10 females and eight males); and (3) 13 cases of suspect fetal or neonatal atelectasis (six unknowns, four females, and three males). Atelectasis was the second most important cause (14.9%) of mortality of newborn calves on a 3-yr basis, 17.5%, including suspect cases (Tables 3, 4). However, most of this importance was established by the relatively high contribution in 1981 (Tables 3 and 4) for which we have no explanation.

The relative occurrence of calves with essentially whole body weights of less than 4.0 kg was greater than expected among calves with atelectasis than among calves that died of other causes ($\chi^2 = 10.70$, 1df, $P < 0.01$) (Table 35). This proportional high level of nonviable body weights for cases of atelectasis, mostly the neonatal type, seemingly reflects the likelihood of premature births or complications in fetal development being linked with this condition.

We have termed all complete failure of lungs to distend with air as 'fetal atelectasis', which is essentially synonymous with 'stillbirths' but could be caused by undiscerned conditions at the time of birth. We have termed all incomplete distension of the lungs regardless of pathogenesis as 'neonatal atelectasis', which often can be associated with poor fetal development or 'premature births' but also can be caused by undiscerned conditions at about birth or within a short period (1-3 d) after birth.

The congenital form of atelectasis is qualified depending on its pathogenesis as "obstruction" or "compression" atelectasis (Jubb and Kennedy 1970). Bronchial obstruction is the most frequent prelude to atelectasis (Smith and Jones 1966). In fetal or congenital atelectasis the lungs are small as in the fetus, but because of dilation of the alveolar capillaries they are dark, reddish blue in colour. The lungs are of fleshy consistency and do not float, when placed in water. Fetal atelectasis as is found in the "stillborn" fetus is often referred to as "primary" atelectasis. In such cases, apart from capillary engorgement there is no significant departure from the fetal state. The alveoli are partially distended with fluid as they normally are in the fetus.

The factors causing fetal atelectasis are not well understood. The condition occurs in all mammals including man (Smith and Jones 1966, Jubb and Kennedy 1970). In a study of lamb mortality in Montana, atelectasis was the third highest (14.3%) cause of mortality (Safford and Hoversland 1960).

Neonatal (secondary) atelectasis is usually patchy and is frequently seen affecting groups of lobules and occasionally much of the lung. Microscopically the alveolar walls are closely approximated and the alveoli contain some fluid, debris and phagocytic cells. The sectioned surface is liver-like and free blood is readily expressed from it (Jubb and Kennedy 1970).

The cause of neonatal atelectasis is the blockage of a bronchus or a group of bronchioles by mucous secretion or owing to weak inspiratory movements a portion of the lungs fails to become distended with air. The air contained in the alevoli of the blocked bronchus is absorbed in a short time and the airless alevoli then collapse under surrounding pressures.

Neonatal atelectasis had been attributed to the inspiration of placental fluids at the time of parturition (Smith and Jones 1966, Jubb and Kennedy 1970). It has been suggested that weak calves may lack the muscle tone required to effectively aerate the lungs. Maternal cows with little maternal instinct may possibly be ineffective in grooming and drying off the newborn and thus fail to stimulate the calf's respiratory system.

Disease such as brucellosis may cause abortion or the production of a premature or often weak full term calf (Stableforth, 1959:53-159). A serological survey for brucellosis in the Beverly herd had revealed only two positive and two suspicious titres (CWS, unpubl. data). Lent (1966:714-715) while studying caribou calving behaviour in northwestern Alaska observed several cows in 1962 and 1963 with calves that were either stillborn or died soon after birth. He suspected that at least some of the stillbirths resulted from cows being infected with brucellosis, but no exact determinations were made. McEwan and Whitehead (1972) found a connection between pre-parturient food intake and vitality of calves. Espmark (1980) also suggested that poor nutrition of the dam may result in weak calves. Espmark (1980) also showed nonsignificant evidence for a longer gestation period in undernourished females. A causal effect between bad winter conditions for pregnant cows and calf mortality the following spring was demonstrated in a 9-year study of a Swedish domestic reindeer herd (Rehbinder 1975 in Espmark 1980). Taylor et al. (1979) postulated that selenium deficiency could contribute to stillbirths, weak calves or other reproductive problems. Skoog (1968:564) noted that stillbirths are not numerous but they are encountered commonly on the calving grounds although in 10 years of study, be found only two pregnant cows in which the fetus probably would have been stillborn. Many of these factors could contribute to atelectasis in barren-ground caribou.

One stillborn calf was delivered by one of 10 well nourished penned cows and none of the calves delivered by nine undernourished cows were stillborn in a Norwegian study (Espmark 1980). This condition, seemingly suggests that reason(s) other than the quality of nutrition must be operative in causing stillbirths. We have also reached this conclusion empirically, based on the generally well developed appearances on most stillborn fetuses.

Our observed rates of atelectasis (Tables 3, 4) are hitherto unreported. Most likely, however, atelectasis (other than observed stillbirths) in dead caribou calves had gone undetected because the lungs were not examined for the condition. For example, in 1958, pathological examination of lung tissue was done for only seven calves; apparently the lungs from the 100+ dead calves found by Kelsall's field men in that year were not examined (Kelsall 1960). The lung tissue from six of the seven calves examined revealed degrees of atelectasis (Kelsall 1960:115-116). Had the lungs of the 100+ dead calves been examined, it is possible that a higher rate of atelectasis would have been found in Beverly caribou calves in 1958.

Methods used in the current (1982-1985) study of the calf mortality in the Porcupine caribou herd in Alaska are biased against finding stillbirths and also neonatal atelectasis as the researchers start by capturing healthy, live calves already one or a few days old (Mauer et al. 1983, Whitten et al. 1984). Supplemental findings from unmarked calves on the Porcupine calving ground might include atelectic ones, but to date, samples of unmarked calves have been small and atelectasis has not been detected or reported (ibid.).

Fetal or neonatal atelectasis (in unborn or newborn caribou) is unlikely a manageable form of mortality. That is, if those conditions are related as suggested to the physical condition of the dam, which is governed by the quality and quantity of her forage intake, we cannot control it. The only form of range management that is likely to be practised is forest fire control on the winter range of the Beverly herd. There is, however, no evidence to suggest that Beverly caribou were nutritionally stressed during 1981, 1982, or 1983. The existing data show that Beverly females had high nutritional status and experienced high rates of pregnancy in those those three springs (D.C. Thomas, unpubl. data).

There is one supposition that could be offered to speculate on a manageable situation where the occurrence of, at least, neonatal atelectasis could be reduced. That is, if neonatal atelectasis results from the inspiration of placental fluids at parturition - then, the possibility exists that any human-caused disturbance at the time of calving could lead to an increased occurrence of neonatal atelectasis. The regulation of human activities associated with mineral exploration on calving grounds has been attempted (Gunn 1984) but regulation of all human activities is difficult.

1.6 Separation or abandonment (malnutrition/starvation complex)

We found 14 dead calves that we assigned to this category of death (eight males, six females). Separation from or abandonment by the maternal cow leading to the death of the calf from a malnutrition/starvation complex was the fourth most important cause (6.2%, n = 225; 5.5%, n = 257) of mortality of newborn calves on a 3-yr basis (Tables 3, 4). We found no predisposition to death due to sex for calves in this category; most (57.1%) of the calves in this category were <4 d old at death.

We assume that calves die from the lack of their mother's nourishment (milk) and not from the lack of forage; so we refer to the cause of death as a "malnutrition/starvation complex". Starvation is defined as death caused by the lack of anything to eat (empty stomach) and death by malnutrition as the result of eating food that does not provide enough or any nourishment (forage in the stomach but no milk). Death usually results from malnutrition rather than starvation which actually, rarely occurs in the wild (cf. Mautz 1978:344).

Deaths in this category result from a combination of causes: first, the calf becomes separated from its mother likely through abandonment, wolf harassment, or human activities. Then, if the calf is not killed by a predator, it subsequently succumbs to a malnutrition/starvation complex which is the proximal cause of death.

Pneumonia can often be a contributing factor to the deaths of newborn calves that have become separated from their mothers. The pneumonia follows the general deterioration of the calf as it suffers from malnutrition/starvation. Regardless of the proximal agents (malnutrition, disease, or predator) involved in the actual deaths, the primary cause is separation of the calf from the cow.

When the calf is found alive, it seems that separation from the maternal cow as the primary cause leading to the subsequent deteriorated state then death of the calf is a valid assumption, if the following conditions are met. (1) The calf was not attended by a maternal cow; or no group or aggregation of caribou was within, at least, a kilometre of the calf when found. (2) Postmortem examination revealed evidence of malnutrition/starvation or a malnutrition/starvation/pneumonia complex. (3) No evidence of other physiologcial complications; pathological disorders; or trauma from predation or injury could be detected. The basic underlying assumption in all of these cases is that the calf would have died from a malnutrition/starvation complex or a malnutrition/starvation/pneumonia complex, although it could have been killed by a predator (or scavenger, if the calf was comatose) had it not been caught by us.

Assigning the cause of death as separation or abandonment from the maternal cow followed by a malnutrition/starvation complex can be misleading for calves that are found dead. Perhaps, such an error in correctly determining the cause(s) of death is most likely to occur when the calf's lungs or most of them are missing from the carcass. This is especially true, if the calf took several days to succumb to respiratory complications brought on by neonatal atelectasis and/or pneumonia. Errors in detection could still occur even if lung tissue was still in the carcass. If the calf had been dead for several days darkening of the lung tissues from postmortem change could mask the presence or severity of a respiratory disorder. Also, the infected area(s) may appear relatively small and suggest that the condition only partially contributed to the calf's death. Thus, if no maternal cow was present or no group of caribou was seen nearby and the calf appeared debilitated from malnutrition, the evidence would misleadingly favour separation from the mother as being the primary reason for the calf succumbing to a variety of disorders.

When a calf carcass is found that exhibits signs of malnutrition; the lungs are missing; and no other evidence of pathological conditions or physiological disorders can be detected, several possible cause(s) of death pertain to the probable determinations. Therefore, we offer the following qualitative procedures (Table 36) to standardize such evaluations and classifications of the most likely cause(s) of a calf's death, until knowledge is gained that would allow further refinement of such determinations. We recommend that suspect cases be classified according to the evaluations presented in Table 36 to standardize speculation.

Various reasons for a maternal caribou's abandonment of her newborn calf or the separation of a cow from her calf have been discussed (e.g., Banfield 1954, de Vos 1960, Pruitt 1960, Lent 1966, Kelsall 1968, Skoog 1968, Bergerud 1974b, Miller and Broughton 1974, etc.). Ten suppositions that have received general acceptance in this literature follows. (1) Abandonment occurs because a cow is a primiparous individual (usually a 2- or 3-yr-old, calving for the first time) that is not truly aware of, or adjusted to, the state of parturition. (2) Abandonment occurs because a young cow calving for the first time, especially after the peak of calving when the caribou are forming or in large aggregations, may retain a strong social tie with her group and fail to establish a bond with her newly dropped calf. (3) Abandonment occurs because a cow (primiparous or multiparous) may have some physiological (more likely primiparous individuals) condition or pathological disorder that results in irritation during the birth process, and thus causes the cow to desert. (4) Abandonment occurs because a cow may develop a mammary infection or disorder such as mastitis that puts her off nursing or she cannot produce milk, and thus the cow becomes irritated or loses her maternal instincts and she deserts her calf. (5) Separation or abandonment occurs from intensive harassment of a cow-calf pair or more likely a calving aggregation by a large predator - wolf or grizzly bear. (6) Separation of abandonment occurs as a result of aircraft, snow mobile, or all-terrain vehicle pursuit and harassment. (7) Separation or abandonment occurs from crowding, mixing in the water and by losing contact after making water crossings, especially later in the summer (July-August). (8) Separation or abandonment (mainly when <1-d-old calves are involved) occurs when a human captures a calf or makes prolonged contact (for whatever reason) with a calf. (9) Separation occurs because of the calf's own activities: e.g., exploratory behaviour. (10) Separation occurs because the mother and her young become asynchronous in their activities: e.g., calf remains sleeping while its mother moves off foraging or with her social group; calf moves off while engaged in play with other calves; strange cow (most likely a deprived mother) lures calf away from its unelerted mother; etc.

Skoog (1968:572-573; 576; and elsewhere) recounts early Alaskan reindeer reports that identify young reindeer cows as exceptionally poor mothers, lacking maternal behaviour, forming only weak bonds with their offspring; and thus, submitting their calves to high mortality.

Lent (1966) believed maternal cows were more likely to desert their newborn calves, if the calves were born near or after the end of the calving season. As noted by Skoog (1968:531), "Pertinent to Lent's (1966) findings also is the fact that young reindeer cows (i.e., those breeding as calves and yearlings) give birth to their calves 2-4 weeks later than the peak of calf-drop for adult animals (Jackson, 1898, 1903)." In six seasons on the calving grounds of the Nelchina caribou herd in Alaska Skoog (1968:530) never saw a "young" cow searching for her "lost" calf but he noted that adult cows spent considerable time doing so. The implication is that probably very few calves born to cows bred as yearlings survive the first week of life (Skoog 1968:531).

Miller and Broughton (1974) classified 12 calves (21.1%) as having died as a result of being separated from or abandoned by their maternal cows. One calf listed under death due to malnutrition should have also been included with the 12 calves. Thus, 13 dead calves found on the Kaminuriak calving ground in June 1970 succumbed, apparently, initially because of separation or abandonment from their mothers. However, based on our criteria only five of those 13 calves would be classified as definite cases of separation and/or abandonment. Seven of the eight remaining calves would be classified as suspect cases of neonatal atelectasis possibly associated with separation or abandonment by the maternal cows; and the one remaining calf would be classified as a suspect case of separation or abandonment with possible complications from neonatal atelectasis or pneumonia. Therefore, separation from or abandonment of calves by maternal cows on the Kaminuriak calving ground in June 1970 was involved in at least five (8.8%) cases and as many as 13 (22.8%) cases. However, at least eight of the calves were probably predisposed to death because of respiratory complications that may have also influenced or even caused their separations from their maternal cows.

Recent results from an Alaskan study of calf mortality, in about the first month of life, using mortality sensing radio-collared calves, in the Porcupine caribou herd suggests that natural abandonment ranged from 16.7% (2) of 12 dead calves in 1982 (Mauer et al. 1983) to 27.3% (3) of 11 dead calves in 1983 (Whitten et al. 1984). Their results are not strictly comparable because their calves ranged from a few days to 3 weeks of age.

In Russia, Baskin (1983) compiled mortality on domestic reindeer calves from 1934-54. In his comparison of factors causing death of newborn reindeer calves during the first month of life on tundra versus taiga he found abandonment by the maternal cow accounted for 16.6% (n = 4797) on tundra and 18.0% (n = 4926) on taiga.

Espmark (1980) studied effects of maternal prepartum undernutrition on early mother-young relationships in 19 pluriparous female penned reindeer in Norway. He found that for calves from undernourished cows: (1) there was a tendency to be somewhat physically retarded at birth; (2) birth weights were relatively low; and (3) growth during the first 4-5 months was relatively slow. Also, he found that undernourished mothers tended to be relatively less concerned for and tolerant of their calves. Espmark's (1980) findings support our supposition that much of the apparent abandonment of calves is by young, primiparous cows. Young cows are probably the least well nourished and in the poorest physical condition of all the breeding cows (with the possible exception of extremely old cows). In years of severe winters, however, even prime-aged, multiparous cows also may be undernourished. Data to support this supposition are still lacking.

1.7 Patho-physiological

We found 15 dead calves that we assigned to this category of death (nine males; four females; and two of indiscernible sex). Death of calves resulting from pathological conditions or physiological disorders was the third most important cause (6.7%, n = 225; 5.8%, n = 257) of mortality of newborn calves on a 3-yr basis

(Tables 3, 4). We found no predisposition to death due to sex for calves in this category; most (86.7%) of the calves in this category were <4 d old at death.

Specific pathological or physiological conditions (other than pneumonia) were of low occurrence and varied, especially between years. Therefore, all calves that died of such conditions except pneumonia were placed in the collective patho-physiological category to better allow direct comparisons between samples.

The most common causes of death (7 of 15 cases) in this category was shock, stress, or drowning from entrapment in frigid waters or slushy mires along the shores of lakes and streams, but six of those seven cases occurred in 1983.

An abrupt warming trend in the second week and the seasonal lack of rain on the calving ground created and adverse environment in June 1983. The slush mires created by melting deep snowbanks along the shores of lakes, rivers, and streams were death traps for newborn calves in June 1983 for about 10 d, and the six dead calves were found on 10, 11, and 13 June. Calves drowned, died of fatigue, stress, or shock while trying to traverse these slush mires. Although these conditions for potential entrapment and subsequent death most likely occur in all or most years on the calving ground during late calving or early postcalving, they probably were not as bad in most years as in June 1983.

Kelsall (1960:146) referred to calves mired in unseasonable deep snow as one of the examples of adverse weather and a late season indirectly causing calf mortality. The slush mires, however, would occur regardless of the lateness of the season because snowbanks are always present during calving (the important consideration is whether they are firm or slushy). It is more a matter of how fast the snowbanks break down after becoming slushy. In fact, a late season would likely prevent or at least greatly reduce this type of mortality because the snowbanks would stay hard packed or refreeze 'nightly' during early June; thus, allowing the newborn calves to traverse them without difficulty. By late June, the older calves should be better able to cope with the slushy areas in a late season.

Pruitt (1960:30) observed that caribou on the Beverly calving ground in 1958 avoided soft snow areas when travelling during the thaw. He noted that when caribou did attempt to cross deep soft snow areas, "...individuals frequently broke through the snow, went in up to their bellies and had trouble getting out (Pruitt 1960:30). Pruitt (1960:30) also saw a wolf pick up a calf carcass that had become mired in soft snow and died. Bos (1974) watched the difficulty with which newborn calves followed their mothers across remnant snowbanks and speculated (p. 17), "Should newborn calves have to transverse large areas of deep soft snow, the likelihood of calf mortality would become very real.".

Mortality of newborn calves from specific environmental conditions such as these will occur annually but at different levels from year to year. Possibly, the benefit of good weather to calf survival outweighs the direct loss of calves to the slush mires unless other agents such as wolf harassment or human activities precipitated movements, especially panicked movements, which could increase this type of mortality.

Other more varied and less frequent conditions leading to deaths placed in this category included: (1) accidental trauma or intraspecific strife (Calf being stepped on or kicked by the maternal cow or some other caribou); (2) malnutrition/starvation, due to maternal cow's death, or apparently as a result of odd articulation of calf's foreleg (probably preventing calf from keeping up with its mother), or apparently due to calf's 'parrot mouth' condition (probably interferring with or preventing nursing); (3) broken leg (calf found alive but would have eventually been taken by a predator or succumbed to a malnutrition/starvation complex); (4) peritonitis, associated with infection of umbilical cord; and (5) hydrocephalus condition - abnormal displacement of frontal bones of skull (proximal cause of death undetermined because carcass was too decomposed to obtain brain tissue for histo-pathological examination).

We found no evidence of heavy parasite loads and only one possible *Escherichia coli* infection in this study. Miller and Broughton (1974) found a weak, uncoordinated, diarrhetic, 8.6 kg, 10 to 14-d-old, male calf in the Kaminuriak herd who's mother had *E. coli* in her milk. The cow was suffering from necrotic vulvitis and inflammation of the vagina and uterus. Miller and Broughton (1974:9) concluded that, "The metritis and vaginitis may have caused the cow to go off milk production. When the cow came back into milk prodution, the calf was too weak to nurse, or possibly because of the *E. coli* mastitis did not like the flavour of the milk and refused to nurse."

Thing and Clausen (1980) and Clausen *et al*. (1980) working on caribou in Greenland report epidemic infection and heavy parasitic loads leading to massive die-offs of calves during their first summer of life. Thing and Clausen (1980) estimated that 50% (1977) and 30% (1978) of the calves born north and east of Sdr. Strømfjord in southwest Greenland died at 2-3 months of age from *E. coli* infection. Thing and Clausen (1980:434) stated that, "The first year most of the sick calves had diarrhea and were loaded with parasites, i.e., coccidiae, tapeworms and roundworms. The next year the calves were found with diarrhea, were limping and had swollen joints due to infection of *E. coli*, mainly type 0 55.". They believed that poor condition among cows in spring led to weakened calves in summer that were highly vulnerable to any pathogens; thus, *E. coli* was only the terminal cause of death. After a third year of this study in Greenland, Clausen *et al*. (1980) reported that the average calf:cow ratio for 1977-79 was 69.6:100 in the third week of June to only 24.3:100 at the end of August. However, they reported that only 10-20% of the calves had suffered diarrhea followed by polyarthritis that was associated with a massive infection of *E. coli* O-group 55. They concluded that the diseased condition was probably brought on by concentration of caribou on preferred foraging areas, "golf greens" of blue grass (*Poa pratensis*).

Although caribou are relatively 'clean animals' with regards to parasites and diseases, they (newborn and others) can be burdened with or infected by quite a wide array of parasites, diseases, and disorders (Banfield 1954:33-43, Kelsall 1968:268-274, Skoog 1968:590-610, Neiland and Dukeminier 1972:1-47).

Skoog (1968:565-566) noted occasional malpresentation of the fetus; and that retention of afterbirth varied markedly among herds in Alaska. Lent (1966:715) also noted the retention of afterbirth in Alaskan caribou. Brucellosis appeared to be a problem in the Arctic herds in Alaska (e.g., Neiland et al. 1968, Skoog 1968, Neiland and Dukeminier 1972). Brucellosis has never been found except at low occurrences, in Canadian barren-ground caribou herds (Broughton et al. 1970) but even epidemic levels could have escaped detection. The incidence of almost all diseases in caribou is unknown.

In Alaska dried shrivelled afterbirth, signs of excessive bleeding, and stunted or weak calves were reported in caribou herds in which brucellosis was present (Witter 1981). In our studies on the Beverly caribou calving grounds we did not observe retained placentas or excessive hemorrhage from the vulva. A few cases of hygroma, large swelling of the carpal joint (which is common in cattle (Bovis spp.) infected with brucellosis) have been reported from the Beverly herd (CWS, Pathology Sect., unpubl. data).

Over 200 serum samples have been tested from the Beverly herd for brucellosis and only two positive and two suspicious reactions have been detected (CWS, Pathology Sect., unpubl. data). This low level of serological evidence of brucellosis would indicate that brucellosis is not significant in the Beverly caribou in terms of effect on reproduction.

At parturition, or abortion an animal infected with brucellosis will shed large numbers of brucellae in the uterine discharges, placental tissues, and the calf. These discharges will be the main source of infection for susceptible animals.

The spacing of parturient females on the calving grounds is probably an effective way of initially minimizing exposure of susceptible animals. Movements from the calving grounds shortly after calving could also reduce exposure of susceptible animals to a potentially infected environment. Also by the time the caribou have aggregated the uterine discharges probably will have ceased, further reducing potential for distribution of the organism.

In the late 1950s and early 1960s brucellosis was a problem in Canadian reindeer maintained in close herding. When a dispersed type of herding was introduced the incidence of brucellosis dropped significantly (CWS, Pathology Sect., unpubl. data).

Skoog (1968:595) pointed out, "...the association of caribou mortality with rabies in canids could be a significant relationship with regard to population regulation.". K.A. Neiland in Klein and White (1978) suggested that wolves perpetuate the occurrence of pathological agents in caribou populations by their interactions with caribou and, thus, assure themselves of an easily obtainable food source.

Skoog (1968:564) reported two fetuses with congenital deformities: one of the fetuses was hydrocephalic and had club feet; the other fetus had a distorted vertebral column, cervical vertebrae numbered only four instead of the normal seven and excessive fusion had occurred in the lumbar region and included the pelvic girdle. Bergerud (1971) does not mention any congenital deformities among the 114 young calves he examined in Newfoundland from 1957 to 1967. He does, however, list five (4.4%) calves dead from unspecified physiopathological conditions (Bergerud 1971:37).

Drowning is likely to be more important as a cause of calf mortality during July into August when postcalving aggregations are frequently making water crossings on large water bodies. The most significant example of the possible importance of calf drownings comes from Kelsall (1968:262) who reported the estimated loss of 300 calves among 450 caribou of the Beverly herd that drowned at the narrows in Aberdeen Lake in July 1951.

Calves during their first day or two of life readily stumble and can be accidently knocked over and trodden on or trampled, especially if the animals are frightened or panicked by an approaching predator or human activity. Calves with broken legs are not the only consequence: we found calves with ruptured livers, subcutaneous hemorrhages, and one calf had a liver abscess that may have started as an internal injury after the calf had been stepped on. Skoog (1968:575-576) also commented on calves with subcutaneous hemorrhages from trampling injuries. Curatolo (1975:120) and Roseneau and Curatolo (1976:51) have concluded that large postcalving aggregations of caribou may respond to both natural and man-made factors as a "super organism" and are susceptible to panicked stampeding.

We rarely observed a cow being aggressive to her own calf (cf. Jingfors et al. 1982, Gunn et al. 1983). Cows did, however, occasionally swing their antlers at or kick at strange calves, though no injured calves were seen after such aggression.

de Vos (1960) has been cited as the example of supposed large-scale intraspecific strife among caribou. He found seven dead caribou calves (estimated to be 1-d to 1-week-old which he believed had all, except one, died within the previous 24 h on about a 10-ha area on the Beverly calving ground in June 1958. When he skinned and examined five of the carcasses, he found, "... that all had bruises, two had body punctures, one a broken skull, and another one a broken vertebral column." (de Vos 1960:256). He concluded that the puncture wounds had been made by antlers and that the calves had died from "violence by adult caribou". He (de Vos 1960:256) further speculated that the calves probably had been "lost in the band, tried to attach themselves to strange females, and were violently attacked;" and that "It seemed likely that this cause of mortality was restricted to calves not more than one week of age as older calves are able to elude attacking cows."

de Vos (1960:256) possibly misinterpreted his findings. (1) de Vos possibly ruled out wolf predation because he could not conceive of a wolf killing several calves and not feeding on any of them. (2) de Vos' description of the five carcasses fits well what we saw at sites where excessive wolf kills were made and little or no utilization occurred. (3) antler punctures from the small antler of females are probably indistinguishable from canine tooth punctures by wolves, because of the similar sizes of the ends of antlers tines and wolf canine teeth, and especially because of tissue pliency and movement after wounding. (4) While low levels of aggression by adult females toward newborn calves have been noted in most all studies during calving, no-one else has ever reported an equivalent occasion of massive intraspecific strife between cows and newborn calves which is not to say de Vos did not see an isolated, rare event. Even such a rare behavioural aberration is likely to be strongly selected against in a species that routinely forms large aggregations during and immediately following calving. (5) Although calves older than 1-week may be more able to elude an aggressive cow, our field observations (unpubl. data) suggest that younger calves are also apt at avoiding kicks or antler swips by cows. Also, if cows were often routinely aggressive, they could undoubtedly be quite successful in persisting in running down and dispatching calves 1 or 2 weeks of age or older.

With regards to our skepticism about de Vos' (1960) interpretation of his findings, interestingly Kelsall (1960:47) when considering de Vos' findings stated, "de Vos's assessment of mortality observed differs from the conclusions of the other field men and for that reason it is worth mentioning." Kelsall's (1960:47-48) subsequent comments warrant quotation "These observations [the ones reported in de Vos (1960:256)] were discussed, shortly after they were made, with de Vos and other of the field men. It seemed that something unusual was involved. While all field men had occasionally noted females striking or butting at strange calves, such incidents seemed to be uncommon among calving bands under reasonably normal conditions. In fact, serious intra-band strife seemed to be relatively uncommon at any time. It was supposed that some of the dead calves had died somewhat earlier than de Vos estimated, during periods of adverse weather. With as many as 600 adult caribou on a 25-acre hill, dead or dying calves might easily receive bruises and injuries through trampling. Also, if predators had seriously disturbed so large a herd, the resulting confusion might easily have resulted in injury to young calves, even in fine weather." Kelsall's (1960:48) reasoning about the likelihood of crowding on the hill causing bruising on the calves seems unlikely but it does serve to point out the possible interpretations when evaluating this event.

Pruitt (1960:33) has stated that the 'threat pose' is "a true instinctive action" and serves as a 'flight releaser' even in newborn calves. Thus, it seems unlikely that fatal encounters between newborn calves and strange cows would be a frequent event, as the calves would preceive the warnings that most always precede any aggressive acts.

Maternal cows maintain social stability through the bond with their own calf and by reinforcing the bonds of other cow-calf pairs (Lent 1966) by the maternal cow agonistically reacting toward strange calves. Lent (1966:744) noted that the frequency of actual striking of calves by cows during agonistic interactions was low, 6%. He observed that it was doubtful if any of the kicks were hard enough to cause serious injury and that the calves appeared particularly adept at avoiding agonistic acts. Lent (1966:745) concluded that, "Although under certain conditions calf mortality may result from agonistic interactions, it must be considered relatively rare. Most agonistic activity clearly results in no contact between individuals. Not only is there little contact, there are no long sequence of agonistic behaviour, at least outside of the rutting period."

Skoog (1968:574) believed, however, that young calves especially those <5-d-old received a great deal of abuse during the calving period. Skoog (1968:575) agreed that such mortality from intraspecific strife is usually low but suggested that under some situations (not expounded on) could be significant. However, he only found six calves that appeared to have died from antler punctures and four that had been trampled or kicked to death.

Although the views on intraspecific strife between cows and calves at or about the time of calving vary qualitatively, the consensus is that mortality due to aggression under normal conditions will be low at worst and most likely only negligible, except possibly in rare events. It seems that the only management applicable to minimizing such deaths is through protection of the calving ground to prevent or reduce the occurrence of novel stimuli and thus maintain as stable an environment as possible during calving and the postcalving periods of the calf's dependency on the cow for sustenance (May-September).

1.8 Pneumonia

We found nine calves that apparently died from pneumonia (five females, four males). Pneumonia was the fifth most important cause (4.0%, n = 225; 3.5%, n = 257) of mortality of newborn calves on a 3-yr basis (Table 3, 4). We found no predisposition to death due to sex for calves in this category; most (66.7%) of the calves in this category were <4 d old at death.

We separate pneumonia from other patho-physiological cases because pneumonia is supposedly an important cause of mortality of newborn reindeer calves in years of unfavourable weather - low temperatures, rain and snow, and strong winds (M.V. Nazarov 1926, N. Polyakov 1930, in Pruitt 1961; Zhigunov 1961). The supposed importance of pneumonia for newborn caribou mortality was speculated as the reason for Kaminuriak herd cows to calve on relative dry, rugged terrain (Parker 1972:27-28). Pneumonia may be, however, of some importance even in years with weather favourable to calf survival during calving and early postcalving as a complicating factor in general body deterioration in combination with poor nutrition.

Weather on the calving grounds during calving and early postcalving in 1981, 1982 and 1983 was favorable to calf survival:

little precipitation fell; temperatures were seasonally mild; and winds were seasonally moderate.

Pneumonia in newborn caribou in North America has most likely often gone undetected because the necessary post-mortem examinations were not performed. In 1958 the pathological examination of lung tissue from only seven dead calves revealed that one of those calves had a severe pneumonia (Kelsall 1960:115). Bergerud (1971:37) reported only two (1.8%) young calves with pneumonia out of the 114 dead young calves found between 1957 and 1967 in Newfoundland.

Pneumonia is the conventional term for inflammation of the lungs. Pneumonitis is used in those inflammatory lesions which are characterized by cellular infiltration and proliferation rather than by exudation. The typical bacterial pneumonias are characterized by exudation and consolidation of the lung which may be separated into lobular and lobar. In lobular pneumonia the pneumonia is patchy involving individual lobules. In lobar pneumonia the inflammation spreads rapidly to affect large areas of lobes or entire lobes. Lobular pneumonia may be identified as bronchopneumonia, croupous or fibrinous pneumonia.

Bronchopneumonia is the usual form of pulmonary inflammation. It is particularly common in young calves. Chilling of the body or a part of it lowers resistance and predisposes to pneumonia (Hoerlein and Marsh 1957). Exhaustion and severe hunger also contribute to the development of pneumonia (Hamby and Pounden 1959, Smith and Jones 1966). Atelectasis may initiate or be a sequel to bronchopneumonia (Jubb and Kennedy 1970).

Many cases of pneumonia are fatal as a result of fluid accumulation in the lung alveoli preventing the aeration of the blood. Pneumonia is often fatal even with considerable portions of the lung tissue still functional. Death in such cases is attributed to toxins elaborated by the microorganisms initiating the pneumonia.

Bacteria which cause bronchopneumonia first cause bronchitis and then spread through the respiratory passes to reach the alveoli. The simple catarrhal form of bronchopneumonia may change depending on the causative bacteria resulting in suppuration and abscessation.

The most frequent route for bacteria to enter the lungs is via the bronchi. As bacteria move through the bronchial system infected particles may drop into certain bronchioles and not into others. In the majority of pneumonias the apical and cardiac lobes are the first affected. As the pneumonia process progresses centrally in those lobes there may be involvement of the anterior part of the diaphragmatic lobes. Around each infected bronchiole a pneumonic area develops and eventually involves the entire lobule supplied by that bronchiole. Other bronchioles become infected in the same way resulting in an irregular pattern of hepatized and normal lobules - called lobular pneumonia, or bronchial pneumonia or bronchopneumonia (Jubb and Kennedy 1970).

Fibrinous pneumonia in animals involves mainly the apical and cardiac lobes and the anteroventral portions of the diaphragmatic lobes. Necrosis of lung tissue and abscessation occur frequently in the fibrinous pneumonias of animals. Complications which may result from fibrinous pneumonia are pleuritis, pericarditis and in some cases peritonitis.

Interstitial pneumonia in many cases is merely a pulmonary manifestation of generalized disease such as septicemic diseases characterized by sustained or intermittent bacteremia.

Pneumonias take may forms and originate from varied sources. Therefore, it seems reasonable to persist in maintaining checks whenever possible for evidence of pneumonia in newborn caribou calves. Pneumonia was not a significant mortality factor during this study but that does not mean that it never will be important.

1.9 Unknowns

The fragmentary condition and lack of trauma mostly caused our inability to determine causes of death for the 30 calves classified as unknowns. We have disregarded these cases for which the cause(s) of death were not discerned when evaluating the relative frequencies of causes of death of newborn calves. The relative importance of each cause of mortality only is slightly reduced by including the unknowns.

2. Causes of Cow Mortality

The samples of 7, 6 and 11 dead cows necropsied that died shortly before, during, or shortly after calving in 1981, 1982 or 1983, are too small to evaluate the causes and magnitude of mortality among breeding females of the Beverly caribou herd in those years. The high proportion of cows killed by predators (60.9%) may reflect the actual relative importance of wolves and grizzly bears on parturient or maternal cows at about the time of calving, but cannot be objectively extrapolated.

The 7, 9, and 15 dead cows found during about 44 h, 41 h, and 45 h of low-level helicopter flying supports our field impression that mortality of breeding females either from predation or birth complications was low relative to the total number of breeding females on the Beverly calving ground in 1981, 1982, and 1983. The mortality of breeding females of the Beverly herd at calving time subjectively estimated as follows gives support to our belief that mortality of breeding females was low at calving time.

(1) We located carcasses of only 7, 9, and 15 adult cows compared to 79, 107, and 101 calves during the 3 years.
    (a) We assume equal sightability of carcasses of cows and calves for this consideration.
    (b) We assume that early mortality of calves at calving time was about 10% of the entire calf crop in June 1981-83.
(2) We found 11.3, 11.9, and 6.7 calf carcasses for every one cow carcass, or cow carcasses numbered only 8.9%, 8.4%, and 14.9% of the calf carcasses.
(3) Therefore, we suggest that the level of mortality for breeding females during the calving period was <1.0% in June 1981 and 1982 and about 1.5% in June 1983 of the entire breeding female segment of the Beverly herd (10% early calf mortality x 8.9%, 8.4%, and 14.9% cows), which is in line with our empirical impressions. Although these percentages are low they represent 890, 840, and 1490 breeding females and their offspring removed from the potential growth of the herd, if there were 100 000 breeding cows.

Predation accounted for about 61% (14) of the deaths of the 23 cows for which the causes of death could be determined between June 1981 and June 1983. Nine (64%) of those 14 cows were killed by wolves and five (36%) by grizzly bears. The remaining nine (39%) of the 23 cows died from birth complications and associated pathological problems.

Wolf predation on cows varied as the cause of death from only 14% (1) in June 1981 to 20% (1) in June 1982 to 64% (7) in June 1983. We have no explanation for the apparent among year differences in the relative importance of wolf predation on cows. Grizzly bear predation on cows occurred only in June 1981 and June 1983 and was constant in importance between those years: 1981, 29% (2); and 1983, 27% (3).

There was no direct evidence to indicate that the 14 cows were predisposed to predation by wolves or grizzly bears. All but one (4%, 10+ yr) of these cows were of prime age (74%, 4-8 yr) or young (22%, 2-3 yr). Only one of the 2-yr olds was not pregnant.

The small sample of dead cows offers only some insight into the causes of mortality of breeding female caribou at calving time. Predation and deaths from birth complications were the major, if not nearly the sole causes of mortality to breeding cows during calving in all years (some low level of accidents most likely occurs in all years). Our results document the need to include the mortality of breeding females at calving time as part of any formula for evaluating the population dynamics of any migratory barren-ground caribou herd.

3. Predation and/or Scavenging

Wolves or gulls fed on 78.5%, 86.9%, and 85.1% of all calf carcasses found in May-June 1981, June 1982, and June 1983, respectively. Overall estimated percentage utilization of those carcasses by wolves or gulls was greatest in June 1982, 12.5% less in May-June 1981, and 42.2% less in June 1983. Although the percentage of carcasses fed on in 1983 was higher than in 1981 overall utilization was lower, but there was no significant difference among years in the proportions of individuals fed on ($\chi^2 = 2.58$, 2df, $P > 0.20$).

No clear pattern could be discerned between major parts (deep muscle or viscera) and the percentage utilization class that a carcass was placed in on a weight basis. In 1981, 40.0% (8) of the 20 carcasses with no deep muscle tissue missing were still classified as heavily used at >50% utilized; in 1982, 12.5% (6) of 48 carcasses; in 1983, 6.4% (2) of 31 carcasses. In 1981, 32.6% (14) of the 43 carcasses with deep muscle tissue taken were not heavily used at <50% utilized; in 1982, 38.3% (18) of 47 carcasses; and in 1983, 65.4% (36) of 55 carcasses.

We have no explanation for the among year differences in percentage utilization of the calf carcasses. Perhaps, the differences are mainly a reflection of the unknown temporal relationship in each year caused by the timing of the deaths of the calves and the subsequent location and use by scavengers or the detection by us.

Wolves usually went into the stomach below the rib cage or through the lower part of the rib cage, often biting off some or all of the free ribs). Gulls usually extract viscera and stomach contents from unopened carcasses by making an intercostal hole in the central portion of the rib cage. If the carcass has already been opened by a predator, or other scavenger, gulls will feed from those areas without making new entries. Sometimes gulls extract all the viscera and stomach contents through the small intercostal hole and then leave the carcass to disiccate without any utilization of the deep muscle tissue. Gulls also select eyes and the anterior ends of tongues. In 1982 the gulls took eyes and portions of tongues first, then either abandoned the carcass (in areas where there were an abundance of carrion) or then began extracting viscera and stomach contents. When a wolf takes the tongue from a newborn caribou, it bites in from the bottom and towards the back, often removing the mandible and the entire tongue. When a wolf removes the tongue from an older caribou, it goes in between the posterior ends of the mandibles and rips the entire tongue out, often breaking pieces on the mandibular heel off in the process. Therefore, removal of the tongue by a wolf is easily recognizable. Gulls remove the tongue by entry through the mouth. Therefore, they most often leave the posterior portion (the base) of the tongue in the carcass. Patterns of carcass utilization by wolves and gulls are seemingly stereotyped and similar. Wolves, during these studies, usually took the viscera first; including the stomach contents - milk curds; then, if at all during these studies, they took deep muscle tissue.

If wolf numbers were as low on the calving ground as our sightings suggest, we conclude that each wolf was killing many newborn calves, and that the rate of killing by each wolf is higher than previously thought. Viscera were taken more frequently than deep muscle tissue by predators or scavengers.

The exposure to the easily caught and killed newborn calves; the constant moving of the postcalving groups of caribou; and no known attachment of the wolves with dens all argue against wolves having to return to kills or scavenging on carcasses at that time of the year on the calving ground. Therefore, we suggest that most of the utilization of calves dead from non-predator causes was by scavenging gulls during the 3 years of this study and that also much of the utilization of the wolf-killed calves was possibly by scavenging gulls, especially the consumption of eyes and tongues. Wolves killing newborn caribou calves at calving or during early postcalving may have become specialized feeders, taking only high quality milk curds and some viscera. Or else, wolves are more or less totally consuming some newborn calves and we are not finding any evidence of such complete utilization.

Information on the number of wolves on the Beverly calving ground at calving time is limited. Sightings of wolves obtained during aerial surveys of the calving ground at calving; however, suggest as we have perceived that numbers of wolves are variable among years and usually relatively low (Table 37). For unknown reasons over three times as many wolves were sighted in 1974 and 1978 than in any other year during calving ground surveys (Table 37). The principle wolf denning areas are to the south of the calving ground; therefore, it would be expected that more wolves would have been seen during aerial surveys in years when calving took place south of the Thelon River. However, this pattern of higher numbers during such years does not fully materialize from existing data (Table 37).

Unfortunately, there is not enough supplemental information on possible annual variations in denning success and the status of the wolf population to speculate extensively about the possible factors influencing wolf numbers on the calving ground at calving time in any one year. High pup survival could result in a higher number of young nonbreeding wolves being on the calving ground. Also, successful breeding could increase the number of active dens near the calving ground and thus the hunting of wolves supporting the pups.

We have no evidence of scavenging on calves or adult caribou by wolves on the calving grounds. It seems unlikely that wolves scavenge when they are killing more prey than they apparently can utilize. The extent of scavenging by grizzly bears remains unknown (and no evidence for wolverines was obtained).

Scavenging of carcasses was mainly by gulls in all 3 years although some grizzly bears were present on the calving ground in, at least, 1981 and 1983 during calving and early postcalving and could have accounted for an unknown amount of predation and scavenging on both newborn and adult caribou. Utilization of newborn caribou calves by grizzly bears, whether as a result of predation or scavenging, is apparently so complete that it would mostly go on undetected. Usually only the odd limb is found, and it is assumed that the rest of the carcass was consumed by a bear.

The only noted differences between the occurrence of gulls on the calving ground in 1981 through 1983 were that no glaucous gulls were seen in 1982 and the number of herring gulls subjectively appeared greater in 1982 than in 1981 or 1983. It appears that some gulls have learned to take advantage of the relative abundance of carrion on the calving ground during June of the year. However, herring gulls on the Beverly calving ground should be on the nest by late May (Macpherson 1961, pers. commun.); so only nonbreeders or birds that have lost their nest are likely to be the primary users of this source of carrion. However, only adult birds were seen on carcasses; also, few (probably <5%) of the gulls seen on the calving ground were in juvenile plumage.

Herring gulls in all 3 years and also to a lesser extent glaucous gulls only in 1981 and 1983 were persistent and voracious scavengers, who worked calving and postcalving groups of caribou, apparently searching for remnants of afterbirth and dead individuals. Shortly after calving, gulls worried maternal cows in attempts to feed on the bloodied afterbirth on the ground nearby freshly dropped neonates. On occasion, gulls also tried to approach newborn caribou, not yet able to stand, but the maternal cows rushed at the gulls. No gulls were ever seen to attack healthy live calves, although some hemorrhaged wounds suggest that occasionally gulls start feeding on comatose calves. Gulls also followed cows who had remnants of placental tissue hanging from their vagina. Such cows alerted to the gulls and often trotted short distances to evade the 'hovering' gulls (gulls that flew into the strong ground winds and seemingly hovered near the cows). Sometimes, if the gull was flying within only a metre or so of the ground the pursued cow would turn, rush and occasionally rear up at the gull, who would use the strong ground wind to be carried away from the oncoming cow.

Most of the carcasses scavenged only by gulls were relatively lightly utilized in comparison to other carcasses that apparently were both fed on by wolves and scavenged by gulls. This difference in degree of utilization is the main reason for us being able to observe much of the differences in handling and utilization patterns between gulls and wolves. Increased utilization of the carcass, even by gulls only, would result in loss of most of the characteristic features that allow us to separate scavenging by gulls from feeding by wolves.

Rough-legged hawks were most likely minor scavengers in June of all 3 years. A Sabine's gull was once seen feeding on a carcass of a yearling caribou (1981). Jaegers were infrequently seen and only a few sightings of golden eagles and ravens were made on the calving grounds in June 1981, and 1982 and none in June 1983. Arctic foxes were few and likely at most were only minor scavengers. No active fox dens were seen on the calving ground throughout the study.

3.1 Predators of caribou calves

Wolves, grizzly bears, golden eagles, and lynx (*Lynx canadensis*) are the major predators of caribou calves (e.g., Clarke 1940, Murie 1944, Banfield 1954, Harper 1955, Kelsall 1968, Skoog 1968, Bergerud 1971, Clark 1971, Kuyt 1972, Miller and Broughton 1974, Bos 1975, Curatolo 1975, Miller 1975, Roseneau and Curatolo 1976, Davis *et al*. 1978, Mauer *et al*. 1983, Whitten *et al*. 1984). Wolves were the single most important predator of newborn calves in this study and in the Kaminuriak study (Miller and Broughton 1974). Currently, numbers of grizzly bears, golden eagles, and lynx are too low on the Beverly calving ground to consider them anything other than possible minor predators (no evidence of golden eagle or lynx predation on calves was detected in this study). However, wolves are often replaced in importance as predators on newborn caribou by grizzly bears and golden eagles in Alaska (e.g., Mauer *et al*. 1983, Whitten *et al*. 1984). In Newfoundland where no wolves occur, the lynx is the major predator of caribou calves and other caribou (Bergerud 1971). There are several lesser predators that could in some years and on some ranges prey on newborn caribou: the arctic fox, bald eagle (*Haliaeetus leucocephalus*), black bear, coyote (*Canis latrans*), raven, red fox (*Vulpes vulpes*), and wolverine (*Gulo gulo*).

Wolverines are known predators of reindeer (e.g. Pulliainen 1965, Skogland 1985) in Europe but have been rarely recorded as predators of caribou in North America (Kelsall 1968). We have no recorded sightings of wolverines on the Beverly calving grounds and we found no signs such as tracks or scats nor did we find injuries on carcasses that were not consistent with those caused by wolves or grizzly bears.

The most recent (1982 to present) study of early neonatal caribou mortality in Alaska has been on the Porcupine caribou herd: it is also the first caribou study in North America to use radio collars with mortality sensing transmitters on calves (Mauer *et al*. 1983, Whitten *et al*. 1984). Results from 1982 (Mauer *et al*. 1983) and 1983 (Whitten *et al*. 1984) indicate that predation by golden eagles and grizzly bears is the principle cause of mortality of newborn calves. However, no wolf predation was detected from 1982-84. In 1982 they found 12 of the 23 radio-collared calves and three unmarked calves dead during June: 8 (53.3%) were attributed to golden eagle predation; and one (6.7%) to grizzly bear predation. In June 1983 they found 10 of their 63 radio-collared calves and 13 unmarked calves dead: 13 (56.5%) were attributed to grizzly bear predation; five (21.7%) to golden eagle predation; and one (4.3%) to an unknown predator.

Roseneau and Curatolo (1976:30) had previously suggested that golden eagles, especially non-nesting subadults, were probably the single most important predator of newborn calves on the Porcupine caribou herd's calving ground and early postcalving areas in recent years. They also concluded that grizzly bears were probably the second most important predator of calves, either directly or by killing the pregnant or maternal cows.

Ravens were essentially absent from the Beverly calving ground during June 1981-83 and no attempts at or predation by them on newborn calves was observed. However, ravens have been identified as a predator on newborn reindeer (e.g., Kumlien 1879:78, Flerov 1952:217 in Skoog 1968:618-619; Nowosad 1975) and thus are a potential predator of newborn caribou.

3.2 Scavengers of caribou calves

Although gulls are the principle scavengers of newborn caribou (and all other dead caribou) in this study, all of the above predators could also act as scavengers (although no evidence was found in this study for wolves scavenging on calves or adult caribou). The most likely minor scavengers on the Beverly calving ground include, but are not necessarily limited to, the grizzly bear, arctic fox, rough-legged hawk, jaeger(s); and possibly, though not detected, the wolverine. There is also a number of lesser scavengers that could possibly utilize dead caribou: see Kelsall (1968:51-56) for details.

4. Representation of the Samples 1981-83

A systematic aerial search procedure would allow evalution of the representativeness of the annual samples of dead calves and cows relative to the overall calf crop and the breeding cow segment. To collect adequate samples we would need (1) accurate counts of the number of breeding cows occupying each segment of the search area during calving and early postcalving; and (2) estimates of the amount of time those animals spent on each of those segments. Obtainment of such counts and estimates was not feasible and we would likely obtain a smaller sample of dead caribou, if we carried out systematic searches over the entire calving ground in each year.

Therefore, we decided to carry out unsystematic aerial searches of segments of known relatively high occupation. Application of effort was not always proportional to the assumed relative use of the segments, because the sampling effort was spread over as large an area of the calving ground as possible to maximize both the size and representativeness of the annual samples. Although desired quantification was lacking, the primary objective of the study was adequately addressed - gaining insight into the causes of mortality of newborn caribou calves.

Other studies describing the causes of calf mortality have not detailed their apportioning of sampling effort relative to the distribution of the caribou or the progression of calving. The absence of sampling information is largely attributable to the description of calf mortality being incidental to other study objectives. Some investigators have relied on direct observations of cows and calves (e.g., Curatolo 1975, Boertje 1981) or ground searches by observers for calves (e.g., Lent 1960, Bos 1974). Bergerud (1971) carried out aerial helicopter searches to determine from a cow's behavior ("faithful conspicuous does") if a dead calf was in the area but he did not detail the effort of his unsystematic searches.

Our searching efforts were spread throughout early to late calving and into early postcalving (App. 5) to increase the representativeness of the samples by time. Also, although searching new areas over time might have reduced sample sizes as few carcasses were available in early calving it increased the level of representation.

A quantitative evaluation of the effort required (helicopter time/carcass) to find a carcass (App. 5) is not exact because of the clumped associations of dead caribou and the ground searching carried out to find such clumps. However, the approximations (App. 5) indicate effort over time (but they are confounded by changes in search areas) and they emphasize the expected temporal pattern of an increased number of dead calves with time in each year.

We cannot empirically determine the representativeness of the samples of dead calves found in terms of the entire calf crops in 1981, 1982, and 1983 to the overall early mortality of newborn calves in the Beverly herd in those years. We can, however, examine three possible results of our sampling approach to indicate in what ways the sample might deviate from the mortalities at the population level.

(1) A gull or an Arctic fox, both highly visible white against an essentially brownish background, provide a strong visual clue to the probable location of a carcass. The observers knew that gulls on land, distant from a body of water, could be feeding on a carcass. Also, that gulls seen continuously circling an area likely had something in sight.

(2) While less conspicuous from the helicopter, a maternal cow can, by her behaviour, indicate to an experienced observer the presence of a dead calf. Those behaviour responses are typically a cow that stands more or less in place, often pivoting, back and forth, as a helicopter passes by, or is reluctant to leave the immediate area and only walks or trots about in a deliberate manner, not attempting directional escape.

(3) By experience, observers knew that once one wolf-killed calf or cow was found, it was probable that additional wolf kills would be found in the immediate vicinity. Often, intensive ground searches in these areas would lead to several carcasses: termed, "clumped associations". This phenomenon, clumped associations, raises the possibility that wolf-killed calves were seen in disproportionate numbers in the sample as opposed to the calves that died of non-predator cause(s).

In May-June 1981 we found 82.3% of the calf and 71.4% of the cow carcasses as singles (no other carcass found within 500 m). The remaining 17.7% calves and 28.6% cows were found in only seven clumped associations of carcasses (Table 6). The five clumped pairs occurred as two pairs of wolf-killed calves; one suspect wolf-killed calf and one calf that died of non-predator causes; one calf that died of non-predator causes and a wolf-killed cow; and a grizzly bear-killed cow-calf pair.

The first carcass found in each of four of the seven clumped associations was a wolf-killed calf; it was a calf that died of non-predator causes in one clump; a suspect wolf-killed calf in one clump; and a grizzly bear-killed cow in one clump.

Based on the above three conditions and the data in Tables 6 and 13, we did two sets of analysis: one set which is based on the overall sample of 55 carcasses (Table 38); and the other set which is based on the subsample of 48 carcasses (Table 39) which includes only singles or the first carcass of each clumped association. The influence of clumping by finding more than one carcass in the same immediate location is removed in the second set. In both sets we carried out two goodness-of-fit type tests both of which examined wolf-killed calves versus calves that died from non-predator causes by whether or not gulls were present and whether either gulls or maternal cows (equals any other animal of any kind) were present when the carcasses were found. When tested for only the presence of gulls we obtained no significant differences ($P = 1.00$) in the overall sample

(Table 38). The subsample of singles was not statistically testable (Table 39).

Observed/Expected (O/E) index values for tests when only the presence of gulls was considered, suggest: (1) that relative rates of occurrence were as expected in all categories in the overall sample (Table 38); and (2) that representation by wolf-killed calves that were found with gulls present possibly was greater than expected in the subsample of singles (Table 39). O/E index values for tests when the presence of gulls or maternal cows (all other animals) was considered, suggest: (1) that carcasses from calves that died of non-predator causes and were found with other animals present possibly were overrepresented in the overall sample (Table 38), and (2) carcasses from wolf-killed calves that were found with other animals present possibly were overrepresented in the subsample of singles (Table 39).

Cases of suspected wolf kills represented a relatively large percentage of probable wolf kills in 1981 (37.8%, 14/37). Thus, we compared wolf kills plus suspect wolf kills to non-predator deaths (Tables 40 and 41) as the best measure of the probable importance of wolf predation on newborn calves in June 1981. Again, no significant differences could be found in the comparisons (Tables 40 and 41). O/E index values for tests when only the presence of gulls was considered, suggest that carcasses of wolf-killed calves found with gulls present possibly were overrepresented in both the overall sample (Table 40) and the subsample of singles (Table 41). However, when the presence of all other animals was considered the O/E index values suggest that it was carcasses from calves that died of non-predator causes that were found with other animals present that possibly were overrepresented in both the overall sample (Table 40) and the subsample of singles (Table 41).

In June 1982 we found 40.2% of the calf and 50.0% of the cow carcasses as singles. The remaining 59.8% calves and 50.0% cows were found in seven clumped associations of carcasses (Table 15). The three largest clumps of carcasses occurred once each. The two clumps of three occurred once as three wolf-kills and once as a cow that died from birth complications, her calf that succumbed afterwards to a malnutrition/starvation complex, and a nearby calf that died of pneumonia. The two clumped pairs occurred as two pairs of wolf-killed calves. The first carcass found in each of five of the seven clumped associations was a wolf-killed calf; a maternal cow that died from a ruptured uterus in one clump; and a wolf-killed maternal cow in one clump.

Based on the above three conditions and the data in Tables 15 and 23, we did goodness-of-fit tests as in the 1981 analysis on the overall sample of 90 carcasses (Table 42) and the subsample of 34 carcasses found as singles or as the first carcass of each clumped association (Table 43). When tested for only the presence of gulls we obtained no significant differences for the overall sample (P >0.10) and we could not test the subsample of singles. In both cases, however, the O/E index values (Tables 42 and 43) suggested that contributions were proportionately highest by calves that died of non-predator cause(s) when the carcasses were found with no gull(s) present. When we tested for the presence of gulls or maternal cows (any other animal present) we obtained nonsignificant differences for both the overall sample (P >0.05) and the subsample of singles (P >0.30). Also, the O/E index values (Tables 42 and 43) indicated that relatively, most of the calves that died of non-predator causes were found when other animals were present.

In June 1983 we found 42.6% of the calf and 72.7% of the cow carcasses as singles. The remaining 57.4% calves and 27.3% cows were found in 16 clumped associations of carcasses (Table 25). The four largest clumps of carcasses occurred once each. The two clumps of four occurred once as four wolf kills and once as three wolf kills and one non-predator death. The two clumps of three occurred once as three wolf kills and once as a wolf-killed cow, her stillborn calf, and a wolf-killed calf. The eight clumped pairs occurred as four pairs of wolf-killed calves; one wolf-killed cow-calf pair; one calf that died of a non-predator cause and one calf that died of an unknown cause; and a grizzly bear-killed cow and her calf that succumbed afterwards to a malnutrition/starvation/pneumonia complex.

The first carcass found in each of 12 of the 16 clumped associations was a wolf-killed calf; it was a calf that died of non-predator causes in two clumps; a calf for which the cause of death could not be discerned in one clump; and a wolf-killed maternal cow in one clump.

Again, we applied goodness-of-fit tests on the overall sample of 92 carcasses (Table 44); and the other set based on the subsample of 53 carcasses found as singles or as the first carcass of each clumped association (Table 45). When tested for only the presence of gulls we obtained no significant differences for the overall sample (P >0.30) or for the subsample of singles (P >0.50). In both cases, however, the O/E index values (Tables 44 and 45) suggested that, if anything, contributions were proportionately highest by calves that died of non-predator cause(s) when the carcasses were found with only gull(s) present. When we tested for the presence of gulls or maternal cows (any other animal present) we obtained significant differences for both the overall sample (P <0.01) and the subsample of singles (P <0.02). Also, the O/E index values (Tables 44 and 45) indicated that relatively, most of the calves that died of non-predator causes were found when other animals were present and most wolf kills when no other animals were present.

The presence of other animals as visual clues to carcasses when found does not significantly influenced the proportional representation of wolf kills or non-predator deaths in the 1981 and 1982 samples. In 1983, however, the proportional representation of wolf kills versus non-predator deaths by whether or not the presence of other animals helped find the carcasses was significantly different. The greatest overrepresentation being made by calves that died from non-predation causes; wolf-killed calves were overrepresented to a lesser degree, when they were found with no other animals present. Therefore, there is no reason to believe that visual clues to carcass locations markedly influenced the finding of wolf-killed calves over carcasses from calves that died from non-predator causes in any of the 3 years.

In all 3 years the possible influence of clumping on the proportional representation of wolf kills versus non-predator deaths appears negligible (<10%).

In 1981 the percentages of wolf kills to non-predator deaths in the overall sample (Table 38) compared to the subsample of singles (Table 39) suggest that clumping of carcasses possibly caused a 15.3% overrepresentation in the 23 wolf kills. The correction reduces the 47.9% (Table 3) for wolf predation in 1981 to 40.6%. In 1981 a better measure in the proportional representation of wolf kills versus non-predator deaths comes, however, from the comparison of the 23 wolf kills plus the 14 suspected wolf kills to the 32 non-predator deaths. When the overall sample (Table 40) is compared to the subsample (Table 41) the indication is that only a 4.4% overrepresentation in wolf kills might be present. This would change the combined value of 52.9% (Table 4) for probable wolf predation to 50.6%. It therefore seems reasonable to assume that at least 40% and more probably about 50% of the calves that died in the first week of life were killed by wolves in June 1981.

In 1982 the percentages of wolf kills to non-predator deaths in the overall sample (Table 42) compared to the subsample of singles (Table 43) suggest that clumping of carcasses possibly caused a 12.0% overrepresentation in the 69 wolf kills. This would reduce the 76.7% (Table 3) for wolf predation to 67.5%. We had previously suggested that 69.8% was a better measure than 76.7% (Table 3). We now suggest that it is reasonable to assume that about 67% of the calves that died in the first week of life were killed by wolves in June 1982.

In 1983 the percentages of wolf kills to non-predator deaths in the overall sample (Table 44) compared to the subsample of singles (Table 45) suggest that clumping of carcasses possibly caused a 12.3% overrepresentation in the 62 wolf kills. This would reduce the 71.3% (Table 3) for wolf predation to 62.4%. Thus, we suggest it is reasonable to assume that about 62% of the calves that died in the first week of life were killed by wolves in June 1983.

There are, however, at least three areas of weakness (in terms of direct evaluation) in this study. (1) We have no way of directly demonstrating that the relative importance of the various causes of early calf mortality are accurately represented in the annual samples of dead calves. However, analyses of all of the existing data offer no indication that the representation is not correct. Also, our annual samples appear to be of adequate sizes and our sampling over time (calving through early postcalving) and space (annually, nearly all of the core of the calving ground) argue for us having a fair degree of biological confidence in our samples. Therefore, we must assume that our annual samples give good approximations of the relative importance of the various causes of early calf mortality during June 1981-83. (2) We could not obtain a refined measure of the chronology of death among newborn calves, because we could not use mortality sensing radio collars on calves or on adult cows. However, as most of the mortality of newborn calves reported in this study occurred during the calf's first week of life, this condition is of minimal concern relative to if we had measured causes of mortality over several weeks or months of the calf's life. The estimated ages of the dead calves indicate that relatively more calves died during the first 3 to 4 d of life than during the second 3 to 4 d of life. Therefore, seemingly, little is lost because of the restricted range of ages of the calves sampled. (3) Our evaluation of the annual loss at the level of the calf crop during 2 of the 3 years of the study are quantitatively poor, because only limited samples were obtained (except in 1982, when the sample was obtained in association with the calving ground survey) of cows with calf at heel or of cows without a calf but with a distended udder in June 1981 and 1983. Empirically, however we believe that our estimates of overall early calf loss are good approximations of what actually occurred in the first half of June in each of those years. Early calf mortality was low in each year and newborn calves were well represented in postcalving aggregations observed in all years of the study. We have no evidence to suggest that our estimates of calf survival based on relatively small calf/cow counts in 1981 and 1983 are not correct; therefore, we accept them as usable indicators of overall early calf survival in those years.

We believe that to maximize the obtainment of data with a high degree of confidence on early calf mortality (i.e., highest assurance of biological soundness and accuracy) a study would require at least the following elements. (1) A large sample of radio-collared calves (preferably, at least 100 calves) for quantitatively documenting the chronology of calf mortality, and for comparison with the sample of unmarked dead calves. (2) A sample of radio-collared pregnant cows for additional evaluation of rates of reproduction and calf mortality, and additional mortality data. (3) Systematic aerial surveys of the calving ground from precalving through calving into early postcalving to determine distributions (densities on both time and space bases) and size of the breeding segment of the herd on the calving ground. (4) Extensive, systematic helicopter searches for dead calves and cows, encompassing at least the entire core of the calving ground from the beginning of calving (therefore, would have to start in precalving period) through early postcalving. (5) Obtainment of large samples from extensive, systematic ground counts of cows with a calf or without a calf but with a distended udder (also with or without antlers, although this character can be misleading as an indicator of pregnancy, at least, in some years) to evaluate calf production and survival. We realize, however, that such a study is not likely to be forthcoming, mainly because of the extremely high costs and other resource demands necessary to carry it out over a necessary time frame of several years.

5. Mother-young Bond

In 1981, maternal cows were still standing over seven of the calf carcasses when found. Four of those carcasses had not been scavenged (one calf was still alive) but the other three had been fed on either by predators or scavengers. Two of those three calves had been killed by wolves and the third was suspected to be a wolf-kill also. Each of the three carcasses when found had several gulls feeding on them.

In 1982, maternal cows were still standing over 10 of the calf carcasses when found. Seven of those carcasses had not been scavenged but the other three had been fed on either by predators or scavengers. One of those three calves was a wolf-kill with three gulls on it when found. One of the other two died of pneumonia and the other one was stillborn (fetal atelectasis): six gulls and one gull, respectively, were feeding on those carcasses when found.

In 1983, maternal cows were still standing over 11 of the calf carcasses when found. Seven of those carcasses had not been scavenged but the other four had been fed on by predators or scavengers. Three of the four utilized carcasses had no gulls present when found: two wolf kills and one suspect case of fetal or neonatal atelectasis. The remaining one, a stillbirth, of those four had two gulls on it when found.

The relative number of unscavenged carcasses with maternal cows standing over them is significantly less than expected when compared with the proportion of calves scavenged with no maternal cows present (Table 46: $P < 0.001$). This condition could have been linked with the fact that significantly more maternal cows were still with calves that had died from non-predator causes than with calves that had been killed by wolves (Table 47: $P < 0.001$). Consideration of only those calves that died from non-predator causes; however, still gives a significant difference (Table 48: $P < 0.001$): less calf carcasses were scavenged when the maternal cow remained with the dead calf (cow was still present when we found the calf carcass). Therefore, this condition seemingly further supports the persistence of the mother-young bond by many maternal cows even after the deaths of their calves (Miller and Broughton 1973). The mother-young bond may persist for several days or more after the death of the calf while the maternal cow defends her calf's carcass from scavengers. On some occasions, however, several or more persistent scavengers are likely successful at limited utilization of the carcass when some scavengers feed while others lured the cow away from the carcass; or while the cow chased others from the carcass site.

Calef _et al_. (1976) cited their observations of barren-ground caribou cows standing over their dead offspring and not fleeing from nearby landings of helicopters as examples of little or no response to helicopter harassment. Calef (pers. commun.) indicated that their discussion (Calef _et al_. 1976) was meant to reflect the tenacity of the mother-young bond between maternal cows and live calves. We disagree; however, that the responses between maternal cows with dead calves and maternal cows with live calves are comparable. When a maternal cow with her dead offspring is disturbed, she can remain standing over her dead calf or withdraw briefly for a short distance, or take flight and abandon the carcass. We believe that because of the ordering of the behavioural repertoire of most maternal cows she has in reality but one choice, that is, to remain at or near her dead neonate. She will do so until sufficiently stimulated to permanently break her bond with the dead calf (Miller and Broughton 1973). When a maternal cow is in the company of a live calf, she can respond to stimuli by flight and the calf will follow. Often the calf is first to take flight and the cow follows, seemingly, often before actually determining the cause.

A maternal cow is, then, more likely to respond by flight from harassing stimuli when in the company of a live calf, that can do likewise, than when "guarding" a dead neonate. The apparent absence of flight as a response by a maternal cow with a dead calf to harassing stimuli is more a measure of the strength of retention of the mother-young bond by the surviving member of the pair, than a direct measure of response to harassing stimuli. The responses of maternal cows with dead offspring should not be used as valid measures of the probable strength of a mother-young or the probable tolerance of a maternal cow with a live calf to man-induced stimuli.

The above discussion also applies to maternal cows with live calves that could not travel with their mothers such as calves immobilized through disease or trauma. A maternal cow with an older calf that could not respond to her cues for flight would be more likely to remain with the calf during periods of harassment than if the calf was only a few hours old when bond formation would probably be weak or incomplete.

The maternal cow licks and feeds its calf within the first minutes of life, initiating the mother-young bond. As the calf grows it solicits care from the mother and further develops the bond. Bonding and individual recognition involve visual, auditory, olfactory stimuli (Lent 1974). A strong mother-young bond is necessary for the survival of the offspring during at least the first 6 months of life (e.g., de Vos 1960, Pruitt 1960, Lent 1966, Kelsall 1968, Skoog 1968, Miller 1982:935).

Bergerud _et al._'s (1984) paper could be misleading in its cited evidence to _suggest_ that the cow-calf bond in caribou seemingly cannot be prevented, broken, or disrupted by human interference of disturbance. Bergerud (pers. commun.) has, however, said that the examples of Newfoundland and Alaskan caribou were not intended to convey such a message and that he had himself published findings to the contrary (Bergerud 1974b:558). The potential for disrupting the cow-calf bond has been described from inadvertent disruptions during studies of behaviour or calf mortality (e.g. Lent 1966, Mauer _et al._ 1983, Whitten _et al._ 1984). Lent (1966:732-733) concluded that, "One or the other _of two_ conditions appeared to account for most cases in which cows failed to reclaim their calves after being caught by taggers. Either the calf was so young at the time of separation that the cow had not sufficient time to identify herself with it, or frequent human activity around the area of separation discouraged the cow from returning and staying long enough to locate her calf." Lent (1966:733) determined during eartagging operations that an undisturbed period of at least half an hour after birth is necessary to insure the return and searching of the cow. "Maternal behaviour patterns that overrule the usual gregariousness and responsiveness to social facilitation of the barren-ground caribou cow must develop almost immediately after birth, if the calf is not to be deserted." (Lent 1966:743). Ponomarev (1938) in Lent (1966:733) reported that, "...abandonment of newborn reindeer calves most frequently occurs when herds were unexpectedly disturbed and that the majority of abandoned calves belong to yearling mothers.". In addition to published observations, many field biologists who have had close contact with cow-calf pairs of caribou at or about the time of calving have experienced occasions when they have inadvertently caused separation between a mother and her young which on some occasions resulted in the abandonment of the calf.

6. Implications of Results for Management

Detailed reasoning of the implications of the findings on wolf predation in terms of possible management practices was requested by CWS as part of the reporting requirements of this project. Therefore, although much of the following discussion goes beyond the scope of the objectives of this study, it is presented to satisfy the above CWS requirement, and should be considered as a CWS position only.

The documented importance, in this study, of wolf predation on newborn calves in the Beverly herd leads to the following consideration of the implications of those findings to management of caribou. The estimated required numbers of caribou to support a wolf on an annual basis (e.g., Clarke 1940, Kelsall 1968, Kuyt 1972) are inapplicable to evaluating what a single wolf might kill in terms of newborn calves. Existing data suggest that wolves are killing newborn calves in excess of their needs (and that they are not subsequently using those kills) and that the impact of even a few wolves on newborn calves can be substantial. Thus, one key to maximizing early calf survival may be in having no or few wolves present on the calving ground.

At the time of initiation of this study, the Beverly Herd was generally believed to be declining in numbers. One management prescription is control of wolves to reduce the numbers of caribou lost through natural mortality. There are several pertient considerations before implementation of wolf control (Fig. 11). Management decisions in the interim may be necessary despite a lack of a sound biological understanding of the wolf-caribou relationship. The main consideration should be that wolf control will not have irreversible impacts on any of the species involved: that is, the target predator (wolves); the benefiting prey (caribou); or any exposed, non-target, susceptable animals.

The record provided by Pleistocene drawings from western Europe confirms that man, wolves, and caribou have existed together for thousands of years (Banfield 1954). Banfield (1954:44) reasoned that, "The relationship between the wolf and the caribou is a close one. In consequence, the wolves of the caribou range are nomadic during the greater part of the year." The wolves on the barren-grounds move with the caribou; thus, probably do not have the same system of territory used by wolves in temperate regions. If northern mainland Canadian wolves hold spatial territories they must be determined by the availability of prey and therefore have to be a mobile territory centred on the caribou over time.

The possibility that wolves dependent upon migratory barren-ground caribou do not have annual fixed spatial territories is important in the application of any wolf control. Any potential approach to wolf control on the ranges of the Beverly herd will have to be tied to the actual locations of the caribou at any given time and not to fixed land areas on those ranges.

One assessment of the consequences of wolf predation can be illustrated on just the newborn calf (<10 d-old) component of the herd, even at the relatively low levels in terms of the total calf crop that were detected in this study (annual wolf predation on older calves and all other sex and age classes of caribou in the herd would be much more significant).

Assumptions

1. The number of Beverly caribou is estimated at 200 000 during the period of the study (based on GNWT Wildlife Management Division, unpubl. data).
2. Females (1+ yr) equal about 60% of the Beverly herd (based on unpubl. data from 1981-82 fall composition counts); therefore, females equal about 120 000.
3. Breeding females equal about 70% of all females (1+ yr) in the herd (based on commonly used 69-72% overall reproduction rates); therefore, breeding females equal about 84 000.
4. Estimated age-specific reproduction rates from the Kaminuriak herd (Dauphine 1976) are applicable as a conservative estimate of those reproduction rates currently (1981-83) being experienced by the Beverly herd: 2%, 1-2 yr; 48%, 2-3 yr; 82%, 3-4 yr; and 89%, 4+ yr.
5. Currently there is a high survival rate of about 66% to the 1st yr (based on 1982-83 recruitments of about 20%).
6. A survival rate of 70% is used for yearlings to the 2nd yr (based on the apparent vulnerability of yearlings).
7. Each cohort (2+ yr) is lost by the 17th yr (based on Miller (1974)). Therefore the survival rate from the 2nd yr to the 3rd yr is 93.3% ((462-31)/462).
8. A caribou at 3 yr of age on the average provides about 36 kg of usable carcass.
9. Replacement values for caribou meat are or soon will be about $26/kg and this price tag could more than double in the next 20 or 30 years. If calf survival during the first year was only 40%, its above replacement volume would be reduced by 40% (these costs include both an estimate for the beef and a 'guestimate' for the likely associated governmental overhead for carrying out the program).

Given

1. For each 1000 calves born, 660 (1000 x 0.66) would live to their 1st birthday; 462 (660 x 0.70) would live to the 2nd yr; and 431 (462 x 0.933) would life to their 3rd yr.
2. Wolves annually kill 5 to 7% of the calves (<10 d-old) of the calf crop (n = 84 000).
3. Detected possible compensatory mortality among wolf-killed calves was 12.8% in this study; therefore, it is reasonable to assume

that at least 80% of the calves killed by wolves would have otherwise lived.

Therefore

1. Had the 4200 to 5880 calves lived that were annually killed by wolves during the first 2 weeks or less of the calf's life, they could have contributed about 1448 ((431 x 0.80) x 4.2) or 2027 ((431 x 0.80) x 5.88) additional 3-yr-old caribou to the herd for harvesting in the caribou's 3rd yr of life.
2. The carcass of a 3-yr-old caribou currently has the replacemnt value of $936 (36 kg x $26/kg) and the near future replacement value will undoubtedly be much higher.
3. Currently, 1448 carcasses of 3-yr-old caribou would have an annual replacement value of $1 355 328 (1448 x $936) or 2027 carcasses $1 897 272 (2027 x $936).

It is interesting to note that (1) if 5000 native people were dependent upon the Beverly caribou herd for their fresh meat supply; and (2) each person eats 0.23 kg (0.5 pounds) of caribou per day, each day of the year (365); (3) they would eat 419 750 kg of caribou (0.23 kg x 365 d x 5000 people); (4) and that caribou meat would be worth $10 913 500 annually at a replacement cost of $26/kg; and (5) even more intersting is that likely near future costs could inflate the replacement value twice the current estimate. The above consideration would require that the currently estimated 1179 hunters on the Beverly range (estimate from draft "Ten year management plan for the Beverly and Kaminuriak herds of barren-ground caribou", October 1984) annually kill 8395 caribou (aver. 7.1 caribou/hunter) at an average overall yield of 50 kg (average for all caribou 3+ years of age) of usable carcass/caribou - a condition that is probably already being realized by users of the Beverly caribou herd.

The 'renewable value' of 1000 female calves killed annually by wolves (or dying of any other cause) over a 50-yr-period is appreciable (Table 49). The high cost of replacement of the total loss of harvestable caribou over a 50-yr-period emphasizes the relative importance of female calf survival to future reproduction in the herd.

The management of caribou should include the maintenance of wolf numbers at levels that maximize human utilization of the caribou resource and at the same time conserve the large herds of migratory barren-ground caribou and the wolf populations associated with them. Specific recommendations for wolf maintenance are few, because much of the concern goes beyond the biological scope of this report into the realm of socio-political considerations.

It is recommended that no wolf control be carried out on the calving grounds at calving time or during early postcalving because it would be ineffective, inefficient and expensive and probably disruptive to cows and newborn calves. The most effective and efficient time to control wolves is most likely in late winter and spring (March into late May) of the year, when many wolves are in close company with the migrating caribou. Possibly, in the absence of using poison baiting, cash incentives to the trappers and hunters to take wolves at that time of the year would be effective. Special aerial shooting teams could be effective on tundra ranges at that time of the year, but costly.

Bergerud (1980:561-564) pointed out that the best evidence for the significance of wolf predation in calf mortality comes from improvements in calf survival when wolf control was carried out in Alaska, British Columbia, and the NWT. Intensive and effective monitoring of recruitments to the caribou herd during and after wolf control will be necessary to demonstrate that the desired effects were produced by reducing wolf numbers.

Wolf control has its place in an intensive caribou management program, but a possibly more efficient, and less costly management exercise than wolf maintenance would be an annual reduction in the harvest of 3+ yr-old female caribou. Reducing the harvest of 3+ yr-old females by 1000 animals yearly (by shooting more males, if necessary) for a 50-yr-period would theoretically put a yearly average of about 3361 additional 3-yr-old caribou at 40% calf survival or 12 101 at 66% calf survival into the Beverly herd (based on the conditions given in Table 49). Thus, retaining a higher number of breeding female caribou rather than saving the same number of newborn calves over an extended period of time (50-yr, Table 49) theoretically would result in 4.3 times greater production of 3-yr-old caribou at 40% calf survival or 2.8 times greater at 66% calf survival (Table 49).

The Beverly herd will have to be larger than the 1982 estimate (ca. 200 000) to sustain future rates of harvest by a human population with the potential to double in the next 20 to 30 years (Hamelin 1979, Schaefer and Steckle 1980, Fuller and Hubert 1981). At that time, any demands in excess of about one caribou per person annually are likely to outstrip the capacity of the Beverly herd, to replenish itself if it remains at the 1982 estimated size or lower.

To reiterate, wolf control is a valid management tool, if it is used in a biologically sound manner. As noted by Heard (1983:47), "Unless the Kaminuriak, Beverly, and Bathurst herds are preserved, wolves will probably [it is not merely a probable condition but an absolute one] disappear from large areas as they have from Southampton Island. Temporary reduction in wolf numbers, as long as it is accompanied by hunting restrictions, should [will] be beneficial to the long-term survival of both caribou and wolf populations."

The documentation of causes of early calf mortality other than wolf predation leads to the following consideration of how those causes of mortality may relate to human activities on the calving grounds. The cow-calf bond in caribou can be prevented, broken, or disrupted by human interference or disturbance, and if sufficient human-induced novel stimuli occurs on the calving ground calf losses will occur. The importance of those calf losses will be governed mainly by the kinds, intensities, frequencies, etc. of the human activities and by the viable alternatives available to the exposed maternal cows that would allow them to avoid or reduce their exposures and still successfully rear their calves. Maximum possible protection of the calving grounds from human interference or disturbance must be part of any successful, biologically sound, intensive management plan for migratory barren-ground caribou. Deaths of newborn calves due directly or indirectly to trampling, mother-young separations or abandonments, intraspecific strife, drownings, fatigue, shock, stress, etc., could be markedly increased by predator harassment and/or human activities. Therefore, every effort should be made to maintain a stable and favourable disturbance-free environment on the calving ground at or about the time of calving. Intensive human activities or development on the calving ground may not be compatible with the successful production and rearing of calves. The cited examples of the absence of calf mortality following human activity on calving grounds (Bergerud et al. 1984) are misleading as those examples are not applicable to large barren-ground caribou herds subject to wolf predation (Gunn 1984). The presence of man, his installations, structures, and activities are likely detrimental to calf production and survival in large barren-ground caribou herds. The ultimate impact will be governed mainly by whether or not viable alternatives are available to the parturient and maternal cows and whether or not they freely make those changes when exposed to novel stimuli.

In summary, the conclusions CWS reaches are as follows.

(1) Intensive management of caribou should include the maintenance of wolf numbers at levels that allow maximizing utilization of the caribou resource by humans; while at the same time conserving the large migratory herds of barren-ground caribou and the wolf populations associated with them.

(2) No wolf control measures should be carried out on the calving grounds at calving time or during early postcalving, because such activities would likely be ineffective, inefficient, and an exceptionally costly place and time period for practicing wolf control efforts, and it could be disruptive to the calving segment of the herd.

(3) Most likely, the most effective and efficient time period to carry out wolf control probably would be in March into late May when most wolves are in close company with migrating caribou (includes wolves that would go to the calving ground and those that would remain in wolf denning areas).

(4) An educational program be started to encourage users to select for male caribou at all times of the year rather than for female caribou during winter and spring. Significantly reducing the annual kill of females could have a marked beneficial effect on the long-term reproduction capacity of the herd. Thus, such action could permit greater annual harvest while at the same time it could allow the herd to grow at faster rates. The herd must grow in order to sustain the likely future demands on it by humans.

(5) The Beverly calving ground (and all other calving grounds) should be permanently protected against human disturbance to help assure maximum early calf survival or to prevent any marked increases in early calf mortality. A relatively stable calving and early postcalving environment is likely essential for maximizing early calf survival. The general lack or low levels of human disturbance in the past cannot be used as a measure of the probable importance of future impacts of man's activities on caribou on calving grounds. The current "Caribou Protection Measures" in use on the Beverly and Kaminuriak calving grounds are at best a stopgap exercise that would be insufficient in the event that a find is made of some nonrenewable resource that is economically profitable for development. Any manager that remains complacent about the possible future impact of humans and their developments on the calving grounds of large migratory herds of barren-ground caribou is running the chance of jeopardizing a valuable renewable resource; perhaps, in an irrevocable manner. The caribou deserve better!

7. Summary Discussion

We think that the study has achieved its primary objective: "gaining further insight into the causes of newborn calf mortality with an emphasis on predation".

Ironically, newborn caribou mortality is a much considered subject and obviously an important one for the caribou biologist and manager to understand, yet the subject has received surprisingly little detailed study on a quantitative basis in North America. Management agencies have mostly opted for doing cow:calf counts to estimate overall losses of calves with less emphasis on investigating the causes of newborn calf mortality. However, without knowing the "whys" of newborn calf mortality an intensive management program is seriously handicapped.

Virtually no other calf mortality studies with the exceptions of the Kaminuriak caribou herd study in 1970 (Miller and Broughton 1974) and the Porcupine caribou herd study in Alaska initiated in 1982 (Mauer _et al_. 1983, Whitten _et al_. 1984) are comparable to this study, and even then the comparisons are only partial. The main problems that do not allow valid overall direct comparisons include (1) few studies have been done solely for the purpose of quantitatively measuring newborn caribou calf mortality; (2) it is not possible to get but a rough approximation (in weeks or just the month of the year) of the ages of dead calves in most studies, and only a few limited samples exist for calves 1-week-old or less at death; and (3) the kinds and numbers of predators involved vary greatly among studies.

We doubt that it is valid to directly compare our findings and those for domestic reindeer in terms of all causes of mortality at the level of the calf crop. However, Baskin (1983:133-134) has compiled mortality data on domestic reindeer calves during the first month of life from 1934-54 in Russia and (if for no other reason, as Baskin (p. 133) pointed out) his sample sizes are so much larger than those that could be obtained from the wild _Rangifer_ that they warrant presentation (Table 50) and some consideration (Table 51).

We grouped the data on Russian domestic reindeer in Table 51 by taking Baskin's (1983:Table 2) data and regrouping (based on numbered categories of death in Table 50) as follows: predation, items (8) and (9) (from Table 50); Atelectasis (stillbirths, premature births, etc.), item (2); Separation/malnutrition, item (3); Patho-physiological, items (1), (4), (5), (6), (7), (10), (11); and we have deleted item (12), unknowns from this consideration. Perhaps, one of the most interesting things to note is that Baskin (1983) lists no deaths specifically due to pneumonia; yet classic Russian reindeer literature (M.V. Nazarov, Reindeer Husbandry, 1926 and N. Polyakov, Reindeer Husbandry and Cooperation, 1930, in Pruitt 1961; and Zhigunov, Reindeer Husbandry, 1961) list pneumonia as a leading killer of newborn reindeer calves (we assume that deaths from pneumonia are lumped under diseases in Table 50).

The overall comparison would be refined by comparing the findings from this study (n = 257) to only those from the tundra calving areas (n = 4197) of reindeer (Table 51). The data (Table 51) suggest that predation was 10.9 times proportionately greater in this study than for domestic reindeer. This difference is most likely from the severe wolf (and possibly other predators) control measures that have been practiced on domestic reindeer ranges in Russia for the past 30 years or more (and possibly the relative effectiveness of those control programs on tundra versus taiga). Deaths due to stillbirths, premature births, etc. appear similar, with those for domestic reindeer, being about 1.4 times proportionately greater than those for Beverly caribou. A marked difference occcurred for deaths initially due to separation from or abandonment by the maternal cow: reindeer yielded 3.3 times proportionately more calves succumbing from this cause than did the Beverly caribou. As Baskin (1983:134) pointed out, reindeer mothers often lack a stable mother-young bond; most likely domestication has indirectly selected against favourable maternal traits in reindeer by herders favouring and keeping tractable animals while culling excitable, responsive individuals. Patho-physiological conditions contributing to deaths of newborn calves in reindeer averaged 8.6 times proportionately greater than in Beverly caribou. Most of the difference appears to be contributed by the relatively high loss of newborn reindeer to diseases (Table 50) and to a lesser extent to adverse weather (Table 50). The greater impact of diseases on reindeer calves most likely relates to practices of domestication and possible crowding on at least some reindeer calving areas and pastures (cf. Thing and Clausen 1980, Clausen et al. 1980).

The influences of many generations of domestication of reindeer; the known and unknown degree of human influences in controlling the distributions of herds and their uses of ranges in time and space; and the severe predator control on reindeer ranges all take away from the above comparisons as they functionally relate to caribou. Therefore, we caution any caribou manager, that the direct use of reindeer data to draw conclusions about free-ranging caribou would probably be misleading. Pruitt (1960) pointed out that there appears to be little reason to suspect that valid comparisons can be made between domestic reindeer and free-ranging caribou on either a physiological or a behavioural basis - we concur.

To reiterate, wolf predation is an omnipresent factor of mortality for the Beverly caribou herd, as for all other migratory herds of barren-ground caribou. Wolf predation is the most important cause of early calf mortality and wolves are the most readily manageable of all detected causes of early calf mortality.

CONCLUSIONS

(1) Weather was basically favourable to calf survival throughout calving and early postcalving periods in all 3 years of the study (1981-83).

(2) Distributions of the 287 dead calves by sex appeared to occur about in accordance with the expected 'secondary sex ratio' in newborn caribou; thus, indicating that neither female nor male calves were predisposed to early deaths because of their sex between 1981 and 1983.

(3) Newborn calves apparently died at greater rates during the first 3 to 4 d of life than during the next 3 to 4 d of life (1981-83).

(4) Wolf predation was the single most important cause of newborn (≤7 d old) calf mortality in samples obtained in each year (1981-83) of this study (3-yr average = 65.3% ± 15.31% S.D.; range, 47.9% to 76.7% - based on 225 dead calves for which the cause of death was determined with certainty).

(5) Overall utilization of wolf-killed calf carcasses by wolves was incomplete; and suggested that wolves were killing in excess of their short-term needs for sustenance.

(6) Evidence was obtained for 'surplus killing' (no utilization of carcass); 'excessive killing' (only slight utilization of carcass); and 'specialized feeding' (apparent preferences for milk curds and viscera over muscle tissue) by wolves.

(7) Newborn (≤7 d) caribou calves are exceptionally easily caught and killed by wolves; thus, essentially only the wolves determine the rates of kill which are likely often much higher than previously thought by anyone.

(8) Previously established estimates of numbers of caribou annually required by wolves are unusable in evaluating wolf-caused mortality of newborn calves.

(9) Representation of wolf-killed calves by sex in the annual samples indicated that calves were not disproportionately predisposed by sex to wolf predation.

(10) Representation of wolf-killed calves by age in the annual samples indicated that wolves appeared to select proportionately more calves 1-3 d old versus 4-7 d old than would be expected to chance alone.

(11) Only 12.8% of all wolf-killed calves exhibited evidence that indicated that they might have died from other causes had they not been killed by wolves - it appears that wolf predation as a form of compensatory mortality was negligible and, thus, only a minor consideration in the evaluation of the impact of wolf predation on newborn caribou calves.

(12) Most calves killed by wolves would have otherwise lived throughout their first weeks of life.

(13) We obtained no evidence of wolves scavenging dead calves or adult caribou during this study, and with one exception all wolves seen occurred as singles or pairs.

(14) Wolves are the most readily manageable of all of the detected causes of early calf mortality in this study.

(15) Grizzly bear predation on newborn calves did not appear to be significant during the 3 years of the study (1981-83). The importance of grizzly bear predation on newborn calves could increase in the future, if grizzly bears expand their ranges northward onto the current area of the calving ground or if the Beverly caribou resume their use of calving areas adjacent to the Thelon River system, especially west of Beverly Lake. Therefore, grizzly bear numbers and locations should be monitored during calving surveys to evaluate the likelihood of increased predation by grizzly bears on the calving grounds.

(16) Atelectasis (fetal - essentially stillbirths but possibly including some deaths that resulted from complications of unknown origin(s) exactly at the time of birth; neonatal - premature births, in utero complications, or complications at or about the time of birth) was the second most important cause (14.9%) of mortality of newborn calves on a 3-yr (1981-83) basis (17.5%, including suspect cases). Minimizing human activities on the calving ground is the only possible management measure that would help safeguard against an increased incidence of some forms of atelectasis.

(17) Mortality of newborn calves from pathological conditions or physiological disorders was the third most important cause of death on a 3-yr basis (6.7%, n = 225, Table 3; 5.8%, n = 257, Table 4). The only manageable aspect of mortality from these causes would be through minimization of human activities that have the potential to force newborn calves into lethal situations (e.g., trampling, entrapment in slush mires, aggressive actions brought on by agitation during fright or flight, etc.).

(18) Mortality of newborn calves initiated by separation from or abandonment by the maternal cow that subsequently led to the calf succumbing to a malnutrition/starvation complex was the fourth most important cause of death on a 3-yr basis (6.2%, n = 225, Table 3; 5.5%, n = 257, Table 4). The management effort to reduce calf separation from or abandonment by maternal cows is the minimization of human activities on the calving grounds at calving and during postcalving.

(19) Mortality of newborn calves from pneumonia was the fifth most important cause of death on a 3-yr basis (4.0%, n = 225, Table 3; 3.5%, n = 257, Table 4). Most likely the relatively low rate of deaths from pneumonia mainly reflects the essentially favourable weather that prevailed during calving and early postcalving in all 3 years of the study.

(20) Wolves were the major predators of adult females on the calving ground, based on our limited sample of parturient or maternal cows found dead.

(21) Grizzly bear predation was not observed in 1982, but was relatively more important on parturient or maternal cows during

June 1981 and 1983 than it was on newborn calves in those years.

(22) We assume that deaths of parturient or maternal cows will occur at low rates in all years from complications and diseases associated with giving birth and from accidents: annually to about 1 or 2% or less of the calving female segment of the herd. The possibility of such mortality to parturient or maternal cows increasing should be monitored during any intensive caribou management program.

(23) Gulls, herring and to a lesser extent glaucous, were the principle scavengers of dead caribou, calves and adults, on the Beverly calving ground during June 1981-83. Gulls heavily scavenged most wolf-killed calves; and may have been responsible for much, if not most, of the carcass utilization, especially the consumption of tongues, eyes, and possibly most of the deep muscle tissue.

(24) Grizzly bears, arctic foxes, and rough-legged hawks were the most probable lesser scavengers of dead caribou on the Beverly calving ground in June 1981-83 during this study. Eagles and ravens were essentially absent from the Beverly calving ground during this study in June 1981-83.

RECOMMENDATIONS

(1) We recommend that helicopter searches for dead calves be routinely carried out as part of the aerial survey program on the calving grounds. Helicopter support is essentially necessary for obtaining adequate calf/cow counts on the calving ground in association with aerial calving ground surveys. Therefore, additional costs for a minimal searching effort for dead calves would not be great. Such an effort could provide an ongoing record of causes of death of newborn calves; and, if some anomalies or catastrophic events took place at or about the time of calving it would more likely be detected when a searching effort for dead calves was in place as part of a intensive management program.

(2) We recommend that the exact number of predators and their locations by latitude and longitude be routinely kept during all future surveys of the calving grounds. Past information on the numbers and distributions of predators on the calving grounds in various years has been so poorly recorded, at least reported, that no worthwhile conclusions can be drawn from the existing information. Better records should be an essential part of any intensive management program: to allow ongoing evaluations of kinds and numbers of predators then currently occupying the calving ground during the calving and postcalving periods.

(3) We recommend that if any future studies of caribou calf mortality at or about calving are carried out, they should include the following elements. (a) A large sample of radio-collared calves (preferably, at least 100 calves) to quantitatively document the chronology of calf mortality, and to compare with the sample of unmarked dead calves. (b) A sample of radio-collared pregnant cows for evaluation of rates of reproduction and data on cow and calf mortalities. (c) Systematic aerial surveys of the calving ground from precalving through calving into early postcalving to determine distributions (densities on both time and space bases) and size of the breeding segment of the herd on the calving ground. (d) Extensive, systematic helicopter searches for dead calves and cows, encompassing at least the entire core of the calving ground from the beginning of calving (therefore, would have to start in precalving period) through early postcalving. (e) Obtainment of large samples from extensive, systematic ground counts on cows with a calf at heel or cows without a calf but with a distended udder (also with or without antlers, although this character can be misleading as an indicator of pregnancy, at least, in some years) to evaluate calf production and survival.

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Table 1

Severest weather days recorded at "Itza Lake" base camp during calving and the first week of postcalving, Beverly calving ground, Northwest Territories, June 1981-83

June	Precipitation		Wind^a		Daily temperatures °C	
	Type	Amount (mm)	Direction	Velocity (km.h^{-1})	Minimum	Maximum
1981						
2	snow	1.0	NE-SE	8-13	-8	14
10	rain	1.0	NE	8-16	-1	7
11	rain	5.0	NE	10-10	-1	9
12	rain	5.0	NE	5-13	1	7
13	rain/sleet	1.0	NE	17-25	0	9
14	snow	1.0	NE	14-20	0	7
16	snow + rain/sleet	8.0	E	12-20	1	6
17	rain	2.0	E	0-8	0	10
18	rain	2.0	NE	10-14	1	10
1982						
4	snow	<1.0	N	10-29	-12	-7
5	snow	<1.0	N	2-9	-12	-3
6	snow	<1.0	E-N	2-9	-8	6
7	snow	<1.0	E	0-9	-3	0
10	snow	1.3	E	19-45	-7	2
11	rain/snow	8.0	NE	0-9	-1	7
19	rain/sleet	8.6	N	19-48	-2	7
20	rain	1.3	NW-N	8-11	-4	-2
21	rain	<1.0	SE-S	16-40	-1	7

Table 1 (cont'd)

June	Precipitation		Wind[a]		Daily temperatures °C	
	Type	Amount (mm)	Direction	Velocity ($km.h^{-1}$)	Minimum	Maximum
1983						
1	snow	<1.0	E-NE	10-22	-1	4
4	snow	<1.0	NW-N	16-51	-2	3
6	snow	<1.0	N-S	8-29	-3	5
8	snow	<1.0	SE	16-29	-1	6
9	snow/rain	<1.0	SE-NW	8-13	0	9
10	rain	<1.0	E-S	8-8	0	9
14	rain	<1.0	N	8-22	1	7

[a] Wind values equal daily range of directions and daily extremes of velocities.

Table 2

Criteria used for estimating ages of caribou calves at death, Beverly calving ground, Northwest Territories, 1981-83

Step	Criterion	Estimated age (d)
1.	Appearance of carcass (subjective)	
1.1	Long-legged and relatively big-headed in proportion to the size of the torso	<1
1.2	Legs and head in proportion to torso	>1
2.	Condition of pelage	
2.1	Incased in placental sac (lungs completely fetal type)	0
2.2	Incased in placental sac (lungs only partially distended)	0-<1
2.3	Pieces of placental tissue adhering to calf's pelage (especially, if lungs only partially distended)	0-<1
2.4	Pelage soaked - hair matted down (not related to ambient wetness)	0-<1
2.5	Pelage dry	≥1
3.	Umbilical cord	
3.1	Present	0-7
3.1.1	Fleshy, and wet to touch	≤1
3.1.2	Drying, and beginning to wither, but still soft	1-3
3.1.3	Dried, and withered	1-7
3.2	Absent	7+
4.	Degree of hoof wear	
4.1	Class 1: Hooves yellowish; soft, translucent cartilage on tips (never walked)	0-<1
4.2	Class 1-2: Hooves blackish with lighter yellowish translucent or opaque areas; cartilage dark and dried on tips; showed no wear (might have walked but never travelled)	0-3
4.3	Class 2: Hooves blackish with some semi-translucent areas near tips; showed no wear (walked but never travelled)	1-3

Table 2 (cont'd)

Step	Criterion	Estimated age (d)
4.4	Class 2-3: Hooves black, showed slight wear or scratches on 3rd or 4th digits (might have travelled some)	1-3
4.5	Class 3: Hooves black; wear on 3rd and 4th digits (minimum travel)	1-3
4.6	Class 3-4: Hooves black; worn on 3rd and 4th digits; dew claws scratched (travelled)	4-7
4.7	Class 4: Hooves black; well worn on 3rd and 4th digits and on dew claws (well travelled)	4-7+
5.	Cheek teeth[a] (milk - p4, p3, p2)	
5.1	p4 - not stained, no vegetation impacted in infundibula	<3
5.2	p4 - lightly stained, little vegetation impacted in infundibula	4-7
5.3	p4 - well stained with considerable vegetation impacted in infundibula	>7
6.	Stomach contents	
6.1	Empty (meconium present in gut) - never nursed - never fed on vegetation	<1
6.2	Milk curds - no vegetation	≤1
6.3	Milk curds, with trace of vegetation	1-3
6.4	Milk curds mixed with a little vegetation	≤3
6.5	Vegetation only (signs of malnutrition and starvation) other criteria suggest (<7 d)	<7
6.6	Some, little, or no milk; considerable vegetation (no signs of malnutrition or starvation)	7+
7.	Whole body weight[b]	
7.1	Less than or equal to 9 kg	<7
7.2	Greater than 9 kg	7+

[a] m1, m2, and m3 not erupted at birth or during first 2 weeks of life; m1 erupting at about 1-month of age (Miller 1974).

[b] Based on whole body weights of caribou calves from the Beverly herd estimated to be less than 7 d old at death in 1981.

Table 3

Percentage frequency of occurrence of causes of mortality to newborn caribou calves, Beverly calving ground, Northwest Territories, May-June 1981, June 1982, and June 1983 (suspect cases and unknowns excluded)

Cause of death	% mortality		
	1981 (n=48)	1982 (n=90)	1983 (n=87)
Wolf-killed	47.9	76.7[a]	71.3
Grizzly bear-killed	2.1		
Fetal atelectasis	10.4	4.4	5.8
Neonatal atelectasis	22.9	5.6	2.3
Separation/malnutrition	6.3	3.3	9.2
Patho-physiological	6.2	5.6	8.0
Pneumonia	4.2	4.4	3.4

[a] In 1982, 69.8% is probably a better overall representative value for wolf predation than 76.7% (see text for reasoning: section 4.1.1).

Table 4

Percentage frequency of occurrence of causes of mortality to newborn caribou calves, Beverly calving ground, Northwest Territories, May-June 1981, June 1982, and June 1983 (suspect cases included)

Cause of death	% mortality 1981 (n=70)	 1982 (n=92)	 1983 (n=95)
Wolf-killed[a]	32.9	75.0	65.3
Suspect wolf-killed[a]	20.0	2.2	3.1
Grizzly bear-killed	1.4		
Fetal atelectasis	7.1	4.4	5.3
Neonatal atelectasis	15.7	5.4	2.1
Suspect atelectasis[b]	11.4		5.3
Separation/malnutrition	4.3	3.3	8.4
Patho-physiological	4.3	5.4	7.4
Pneumonia	2.9	4.3	3.1

[a] In 1982, 69.8% is probably a better overall representative value for wolf predation than 77.2% (see text for reasoning: section 4.1.1).

[b] Fetal atelectasis could not be separated from neonatal atelectasis in all suspect cases.

Table 5

Percentage distribution of estimated ages for 79 caribou calves at time of death, Beverly calving ground, Northwest Territories, May-June 1981

Cause of death (sample size) by sex	% in age class by cause of death				
	0 d	<1 d[a]	1-3 d	4-7 d	7+ d
Wolf predation (n=23)					
female				17.4	
male		8.7	8.7	17.4	
unknown		13.0	17.4	17.4	
Suspect wolf predation (n=14)					
female		7.1	7.1	7.1	7.1
male		7.1		14.3	14.3
unknown		21.4	14.3		
Grizzly bear predation (n=1)					
female	100.0				
Fetal atelectasis (n=5)					
female	20.0				
male	80.0				
Neonatal atelectasis (n=11)					
female		36.4	27.2		
male		36.4			
Suspect fetal or neonatal atelectasis (n=8)					
female		25.0			
male		12.5			
unknown		62.5			
Separation/malnutrition (n=3)					
female				100.0	
Patho-physiological (n=3)					
female			33.3	33.3	
unknown		33.3			
Pneumonia (n=2)					
female				50.0	50.0

Table 5 (cont'd)

Cause of death (sample size) by sex	% in age class by cause of death				
	0 d	<1 d[a]	1-3 d	4-7 d	7+ d
Unknowns (n=9)					
females		22.2			
males		33.3	11.1		
unknown		11.1	22.2		

[a] Some of the calves in this age class that were suspect cases of fetal or neonatal atelectasis were most likely stillborn and would then be 0-d-old at death.

Table 6

Distribution of caribou carcasses by degree of clumping, by death category, Beverly calving ground, Northwest Territories, May-June 1981

Clumping		Number of individuals contributed by each grouping					
Unit	No.	Wolf-killed[a]	Suspect wolf-killed	Non-predator	Unknown	Adult cow	Total
1	70	13	13	30	9	5	70
2	5	5[a]	1	2		2	10
3	2	6					6

[a] Includes one grizzly bear-killed calf that was found along with its mother, who had also apparently been killed by a grizzly bear.

Table 7

Whole body weights from 14 carcasses of newborn caribou calves <1-week-old, by category of death and sex, Beverly calving ground, Northwest Territories, May-June 1981

	Weights (kg)				
N	Mean	Standard deviation	Standard error	95% C.I.	Range
Wolf-killed calves					
5	6.10	1.70	0.76	4.58-7.62	5.00-9.00
females					
1	5.00	-	-	-	-
males					
4	6.38	1.83	0.92	4.54-8.22	5.00-9.00
Non-predation deaths					
9	5.47	1.01	0.34	4.79-6.15	4.00-6.75
females					
4	5.06	0.52	0.26	4.54-5.58	4.50-5.75
males					
5	5.80	1.24	0.55	4.70-6.90	4.00-6.75
Total					
14	5.70	1.27	0.34	5.02-6.38	4.00-9.00
females					
5	5.05	0.45	0.20	4.65-5.45	4.50-5.75
males					
9	6.06	1.46	0.49	5.08-7.04	4.00-9.00

Table 8

Percentage of caribou calf carcasses that were fed on by predators or scavengers that had deep muscle tissue or viscera missing, presented by predator or non-predator causes of death, Beverly calving ground, Northwest Territories, May-June 1981, June 1982, and June 1983

		% fed on		
Cause of death	N	Total carcasses	Deep muscle	Viscera
1981				
Predators[a]	37	89.2	69.7	97.0
Non-predator	32	65.6	61.9	90.5
Unknowns	9	100.0	77.8	100.0
1982				
Predators	71	98.6	48.6	80.0
Non-predator	21	47.6	20.0	40.0
Unknowns	15	100.0	60.0	100.0
1983				
Predators	65	96.9	69.8	84.1
Non-predator	30[b]	56.7	41.2	58.8
Unknowns	6	100.0	66.7	100.0

[a] Includes suspect wolf predation; but not the single, unused grizzly bear-killed calf.

[b] One carcass possibly fed on by an arctic fox only.

Table 9

Approximate estimate of utilization by predators or scavengers of carcasses of caribou calves <1-week-old, Beverly calving ground, Northwest Territories, May-June 1981, June 1982, and June 1983

Year	Sample size	No. carcasses fed on	% in utilization class[c]				
			1-9	10-34	35-49	50-69	70-90
1981	74[a]	60	13.3	18.3	8.3	15.0	45.0
1982	104[b]	93	25.8	19.4	20.4	24.7	9.7
1983	101	86	19.8	39.5	20.9	15.1	4.7

---

[a] Does not include four 7+ d old calves and the single, unused grizzly bear-killed calf.

[b] Does not include three 7+ d old calves.

[c] Calculated for carcasses with deep muscle tissue or viscera missing by assuming: % util. = aver. whole wt. - carcass wt./aver. whole wt. (aver. whole wt. in 1981 = 5.70 kg; in 1982 = 6.09 kg; and in 1983 = 5.42 kg).

Table 10

Summary of carcass utilization of 20 newborn caribou calves that were fed upon by predators or scavengers but had no deep muscle tissue taken, Beverly calving ground, Northwest Territories, May-June 1981

Number of calf carcasses by cause of death	Muscle tissue not missing	Viscera missing				Plus missing	
		All	Most	Some	None	Eye(s)	Tongue
Wolf-killed	3	1	1	1			
Suspect wolf-killed	7	2	3	1	1	3	1
Fetal atelectasis	1		1				
Neonatal atelectasis	1			1		1	
Suspect atelectasis	2	2					
Separation/malnutrition	2		1		1	1[a]	
Patho-physiological	1			1			
Pneumonia	1		1				
Unknowns	2	2					

[a] Only the eyes were scavenged from one carcass - no other muscle tissue, or viscera, or stomach contents was taken.

Table 11

Summary of carcass utilization of 43 newborn caribou calves that predators or scavengers removed deep muscle tissue from, Beverly calving ground, Northwest Territories, May-June 1981

Number of calf carcasses by cause of death	Muscle tissue missing	Plus viscera missing				Plus missing	
		All	Most	Some	None	Eye(s)	Tongue
Wolf-killed	17	15	1		1	2	2
Suspect wolf-killed	6	6				1	
Fetal atelectasis	2			2		2	
Neonatal atelectasis	3		1	1	1	2	
Suspect atelectasis[a]	6	4	2			2	
Patho-physiological	1	1					
Pneumonia	1	1					
Unknowns	7	6		1		2	

[a] Could not separate fetal atelectasis from neonatal atelectasis in all suspect cases.

Table 12

Approximate estimate of utilization by predators or scavengers of 74 carcasses of caribou calves <1-week-old, Beverly calving ground, Northwest Territories, May-June 1981

Cause of death	Sample size[a]	No. fed on	% in utilization class[b]				
			1-9	10-34	35-49	50-69	70-90
Wolf-killed	23	20	15	5	20	15	45
Suspect wolf-killed	11	11	27	9		9	55
Fetal atelectasis	5	3		67			33
Neonatal atelectasis	11	4		50	25		25
Suspect atelectasis	8	8		37		25	38
Separation/malnutrition	3	2	100				
Patho-physiological	3	2		50			50
Pneumonia	1	1		100			
Unknown	9	9				33	67

[a] Unused carcass of calf killed by grizzly bear was not included in this estimate; also, four utilized carcasses from calves estimated to be 7+ d old were not used - three from the suspected wolf kills, and one from the pneumonia cases.

[b] Calculated for carcasses with deep muscle tissue or viscera missing by assuming: % util. = aver. whole wt. - carcass wt./aver. whole wt. (aver. whole wt. in 1981 = 5.70 kg). All 14 carcasses with only eye(s) or tongue missing were placed in the 1-9% utilization class regardless of carcass weight; and four carcasses that were fed on but exceeded the mean weight (one wolf kill, two suspect wolf kills, and one separation/malnutrition) were also put in the 1-9% utilization class.

Table 13

Distribution of caribou carcasses by whether or not any other animals were present when found, by death category, Beverly calving ground, Northwest Territories, May-June 1981

Death category by year	Gulls only	Maternal cow only	Gulls or maternal cows	Gulls and maternal cows	No other animals present	Total
Wolf-killed	5		6	1	17	23
Non-predator	7	3	12	2	20	32
Suspect wolf-killed	5[a]	1	6		8	14
Unknown	3		3		6	9
Grizzly bear-killed			1[b]	1[b]		1
Adult cow	4		5[b]	1[b]	2	7

[a] Includes one carcass with only a rough-legged hawk at it when found.

[b] Includes one grizzly bear and one gull on a grizzly bear-killed cow-calf pair.

Table 14

Percentage distribution of estimated ages for 107 caribou calves at time of death, Beverly calving ground, Northwest Territories, June 1982

Cause of death (sample size) by sex	% in age class by cause of death				
	0 d	<1 d[a]	1-3 d	4-7 d	7+ d
Wolf predation (n=69)					
female		2.9	29.0	2.9	
male		7.2	26.1	10.1	2.9
unknown		5.8	8.7	4.4	
Suspect wolf predation (n=2)					
female			50.0		
unknown		50.0			
Fetal atelectasis (n=4)					
male	100.0				
Neonatal atelectasis (n=5)					
female		20.0	40.0		
male			40.0		
Separation/malnutrition (n=3)					
male			100.0		
Patho-physiological (n=5)					
male		20.0	40.0		20.0
unknown		20.0			
Pneumonia (n=4)					
female			25.0	25.0	
male			50.0		
Unknowns (n=15)					
females		6.7	6.7		
males		13.3	20.0	6.7	
unknown		33.3	13.3		

Table 15

Distribution of caribou carcasses by degree of clumping, by death category, Beverly calving ground, Northwest Territories, June 1982

Clumping		Number of individuals contributed by each grouping					
Unit	No.	Wolf-killed	Suspect wolf-killed	Non-predator	Unknown	Adult cow	Total
1	46	17	2	12	12	3	46
2	2	4					4
3	2	3		2		1	6
4	1			2		2	4
14	1	11		1	2		14
39	1	34		4	1		39

Table 16

Whole body weights from 29 carcasses of newborn caribou calves <1-week-old, by category of death and sex, Beverly calving ground, Northwest Territories, June 1982

	Weights (kg)				
N	Mean	Standard deviation	Standard error	95% C.I.	Range
Wolf-killed calves					
15	6.42	0.87	0.23	5.96-6.88	4.75-7.75
females					
5	6.55	0.57	0.25	6.05-7.05	6.00-7.25
males					
10	6.35	1.01	0.32	5.71-6.99	4.75-7.75
Non-predation deaths					
14	5.75	1.10	0.29	5.17-6.33	4.50-8.50
females					
2	5.63	0.53	0.38	4.87-6.39	5.25-6.00
males					
12	5.77	1.18	0.34	5.09-6.45	4.50-8.50
Total					
29	6.09	1.03	0.19	5.71-6.47	4.50-8.50
females					
7	6.29	0.68	0.26	5.77-6.81	5.25-7.25
males					
22	6.03	1.12	0.24	5.55-6.51	4.50-8.50

Table 17

Summary of carcass utilization of 48 newborn caribou calves that were fed upon by predators or scavengers but had no deep muscle tissue taken, Beverly calving ground, Northwest Territories, June 1982

Number of calf carcasses by cause of death	Muscle tissue not missing	Viscera missing				Plus missing	
		All	Most	Some	None	Eye(s)	Tongue
Wolf-killed	34	11	7	2	14	26	27
Fetal atelectasis	3		1		2	2	
Neonatal atelectasis	2		1		1	1	2
Separation/malnutrition	1				1	1	1
Patho-physiological	1				1	1	
Pneumonia	1				1	1	1
Unknowns	6	3	3			6	6

Table 18

Summary of carcass utilization of 47 newborn caribou calves that predators or scavengers removed deep muscle tissue from, Beverly calving ground, Northwest Territories, June 1982

Number of calf carcasses by cause of death	Muscle tissue missing	Plus viscera missing				Plus missing	
		All	Most	Some	None	Eye(s)	Tongue
Wolf-killed	34	30	4			30	30
Suspect wolf-killed	2	2				2	2
Patho-physiological	1	1				1	1
Pneumonia	1			1		1	1
Unknowns	9	9				9	8

Table 19

Summary of carcass utilization of 68[a] wolf-killed newborn caribou calves, Beverly calving ground, Northwest Territories, June 1982

User category	N	% with deep muscles missing	Utilization class % deep muscles utilized			% with viscera missing	Utilization class % viscera utilized			% with tongues missing	% with eye(s) missing
			All	Most	Some		All	Most	Some		
Wolves and gulls											
	51	66.7		64.7	35.3	100.0	80.4	19.6		88.2	84.3
Gulls only											
	16					12.5			100.0	75.0	81.2
Wolves or gulls											
	68[b]	50.0		64.7	35.3	79.4	75.9	20.4	3.7	83.8	82.4

[a] One of the 69 wolf-killed calves was not used in the table because it was not fed on after it was killed.
[b] One calf carcass was fed on apparently only by a wolf (with only most of the viscera removed).

Table 20

Approximate estimate of utilization by predators or scavengers of 104 carcasses of caribou calves <1-week-old, Beverly calving ground, Northwest Territories, June 1982

Cause of death	Sample size[a]	No. fed on	% in utilization class[b] 1-9	10-34	35-49	50-69	70-90
Wolf-killed	67	66	24	34	12	24	6
Suspect wolf-killed	2	2			100		
Fetal atelectasis	4	3	67			33	
Neonatal atelectasis	5	2	50		50		
Separation/malnutrition	3	1	100				
Patho-physiological	4	2	50				50
Pneumonia	4	2	100				
Unknown	15	15	6	20		47	27

[a] Three calves estimated to be 7+ days old were not included in this estimate: two utilized carcasses of wolf-killed calves; and one unused carcass from the patho-physiological category.

[b] Calculated for carcasses with deep muscle tissue or viscera missing by assuming: % util. = aver. whole wt. - carcass wt./aver. whole wt. (aver. whole wt. in 1982 = 6.09 kg). Descriptive classifications of carcass utilization related to quantitative measures of utilization as follows: (1) minimally used, 1-9%; (2) lightly used, 10-34%; (3) moderately used, 35-49%; and (4) heavily used, 50% or more (50-69% and 70-90%). All 11 carcasses with only eye(s) or tongue missing were placed in the 1-9% utilization class regardless of carcass weight; and four carcasses that were fed on but exceeded the mean weight (two wolf kills, one pneumonia, and one unknown) were also put in the 1-9% utilization class.

Table 21

Percentage distribution of utilization of caribou calf carcasses on an average weight[a] basis, Beverly calving ground, Northwest Territories, June 1982

	% utilization class				
Category	1-9[b]	10-34	35-49	50-69	70-90
Wolf predation (n=69[c])					
Wolf-killed calves fed on apparently by both wolves and scavenged by gulls (n=49[d])	4	39	16	33	8
Wolf-killed calves scavenged by gulls only (n=16)	88	12			
Wolf-killed calf fed on apparently by a wolf only (n=1)		100			
Suspected wolf predation (n=2)			100		
Cause(s) of death unknown (n=15)	6	20		47	27
Non-predator causes (n=10[e])	50	20	10	10	10

[a] The average weight used in this calculation is the mean weight of the 23 whole carcasses found in June 1983 (Table 16:6.09 kg).

[b] All carcasses with only the tongue or eye(s) removed (or less than 0.25 kg of tissue) were placed in the 1-9% utilization class regardless of carcass weight.

[c] One of the carcasses from wolf-killed calves were subsequently untouched by predators or scavengers.

[d] Two of the 51 wolf kills fed on apparently both by wolves and gulls were 7+ d old and were not used in this tabulation.

[e] Total non-predator caused deaths equalled 21 but 11 carcasses in the non-predator category were untouched after death by scavengers.

Table 22

Distribution of ways by which wolves or gulls gained entries to body cavities or removed tongues and/or eye(s) when feeding on the carcasses of 68[a] wolf-killed caribou calves, Beverly calving ground, Northwest Territories, June 1982

% sample size for each combination	Points of entry (X)[b]					
	Rib cage	Abdomen	Flank	Mouth	Eye(s)	Anal area
Carcasses fed on apparently by both wolves and gulls (n=51)						
2.0	X	X	X	X	X	X
7.8	X	X	X	X	X	
2.0	X	X				
2.0	X		X	X		X
25.5	X		X	X	X	
3.9	X		X	X		
2.0	X		X			
2.0	X			X	X	X
13.7	X			X	X	
2.0	X				X	
2.0	X					
3.9			X	X	X	X
5.8			X	X	X	
5.8 unknown[c]				X	X	X
Carcasses fed on apparently by both wolves and gulls (n=51) (cont'd)						
15.7 unknown[c]				X	X	
3.9 unknown[c]						
Carcasses scavenged only by gulls (n=16)						
6.2			X	X	X	
6.2			X		X	
6.2				X	X	X
50.0				X	X	
12.5				X		
12.5 (one with scavenger-made hole in rib cage)					X	
6.2 (nothing taken, but scavenger-made hole in rib cage)						
Carcass fed on only by a wolf (n=1)						
100.0			X			

[a] One wolf-killed calf was not subsequently fed on by predators or scavengers.

[b] (X) equals a point of entry: all (X's) in each row equal the combination of body entries for that percentage of carcasses.

[c] These 13 carcasses were too intensively utilized for us to determine the points of entry through the rib cage, abdomen, or flank.

Table 23

Distribution of caribou carcasses by whether or not any other animals were present when found, by death category, Beverly calving ground, Northwest Territories, June 1982

Death category by year	Gulls only	Maternal cow only	Gulls or maternal cows	Gulls and maternal cows	No other animals present	Total
Wolf-killed	26		27	1	42	69
Non-predator	4	6	13	3	8	21
Suspect wolf-killed	1		1		1	2
Unknown	5		5		10	15
Adult cow	6		6		0	6

Table 24

Percentage distribution of estimated ages for 101 caribou calves at time of death, Beverly calving ground, Northwest Territories, June 1983

Cause of death (sample size) by sex	% in age class by cause of death			
	0 d	<1 d[a]	1-3 d	4-7 d
Wolf predation (n=62)				
female		1.6	27.4	12.9
male		4.9	29.0	11.3
unknown			9.7	3.2
Suspect wolf predation (n=3)				
female			33.3	
unknown				66.7
Fetal atelectasis (n=5)				
female	60.0			
male	40.0			
Neonatal atelectasis (n=2)				
male		100.0		
Suspect fetal or neonatal atelectasis (n=5)				
female		40.0		
male		40.0		
unknown		20.0		
Separation/malnutrition (n=8)				
female			25.0	37.5
male		12.5	25.0	
Patho-physiological (n=7)				
female			42.9	
male			57.1	
Pneumonia (n=3)				
female			66.7	
male			33.3	
Unknowns (n=6)				
females			33.3	
males			16.7	
unknown			50.0	

[a] Some of the calves in this age class that were suspect cases of fetal or neonatal atelectasis were most likely stillborn and would then be 0-d-old at death.

Table 25

Distribution of caribou carcasses by degree of clumping, by death category, Beverly calving ground, Northwest Territories, June 1983

Clumping		Number of individuals contributed by each grouping					
		Calves					
Unit size	No. of clumps	Wolf-killed	Suspect wolf-killed	Non-predator	Unknown	Adult cow	Total
1	51	18		21	4	8	51
2	8	9		4	1	2	16
3	2	4		1		1	6
4	2	7		1			8
5	1	5					5
6	1	5			1		6
7	1	6	1				7
13	1	8	2	3			13

Table 26

Percentage distribution[a] of pneumonic patches in the lobes of the lungs of nine carcasses of caribou calves that died from pneumonia or a combination of pneumonia and malnutrition, Beverly calving ground, Northwest Territories, June 1983

			% pneumonic		
			Diaphragmatic lobes		
Sex	Age (d)	Weight (kg)	Left	Right	Apical lobe
female	1-3	3.75[c]	100	100	20
female	1-3	5.0	20	100	0
female[b]	1-3	5.5	10	10	80
female[b]	1-3	5.75	70[d]	70[d]	70[d]
female[b]	4-7	3.75	25	95	0
female[b]	4-7	6.25	20	40	0
female[b]	4-7	6.5	90	15	50
male[b]	1-3	4.75	100	5	0
male	4-7	6.5	100	100	0

[a] Percentage distribution was determined by visual estimate.

[b] The primary cause of death of these six calves (five females and one male) appeared to be separation from their maternal cows with subsequent actual death from a malnutrition/starvation complex plus complications from pneumonic conditions.

[c] Partial body weight only - carcass had been extensively scavenged.

[d] Lungs were covered with dark purple blotches (samples were taken for histo-pathological examinations in the laboratory and pneumonia was confirmed).

Table 27

Whole body weights from 23 carcasses of newborn caribou calves <1-week-old, by category of death and sex, Beverly calving ground, Northwest Territories, June 1983

	Weights (kg)				
N	Mean	Standard deviation	Standard error	95% C.I.	Range
Wolf-killed calves					
10	5.35	0.88	0.28	4.79-5.91	4.50-7.25
females					
5	5.65	0.98	0.44	4.85-6.53	4.75-7.25
males					
5	5.05	0.74	0.33	4.39-5.71	4.50-6.25
Non-predation deaths					
13	5.48	0.74	0.20	5.08-5.88	4.00-6.50
females					
9	5.69	0.48	0.16	5.37-6.01	5.00-6.50
males					
4	5.00	1.06	0.53	3.94-6.06	4.00-6.50
Total					
23	5.42	0.78	0.16	5.10-5.74	4.00-7.25
females					
14	5.68	0.66	0.18	5.32-6.04	4.75-7.25
males					
9	5.03	0.83	0.28	4.47-5.59	4.00-6.50

Table 28

Summary of carcass utilization of 31 newborn caribou calves that were fed upon by predators or scavengers but had no deep muscle tissue taken, Beverly calving ground, Northwest Territories, June 1983

Number of calf carcasses by cause of death	Muscle tissue not missing	Viscera missing				Plus missing	
		All	Most	Some	None	Eye(s)	Tongue
Wolf-killed	19	6	2	3	8	14	14
Fetal atelectasis	2				2	1	2
Neonatal atelectasis	1				1	1	1
Suspect atelectasis	2	1		1		1	1
Separation/malnutrition	3				3	1	3
Patho-physiological	1				1		1
Pneumonia	1				1		1
Unknowns	2	1	1			2	2

Table 29

Summary of carcass utilization of 55 newborn caribou calves that predators or scavengers removed deep muscle tissue from, Beverly calving ground, Northwest Territories, June 1983

Number of calf carcasses by cause of death	Muscle tissue missing	Plus viscera missing				Plus missing	
		All	Most	Some	None	Eye(s)	Tongue
Wolf-killed	41	35	4		2	33	37
Suspect wolf-killed	3	3				3	2
Suspect atelectasis[a]	3	2	1			1	3
Separation/malnutrition	2		1	1		1	1
Patho-physiological	1			1			
Pneumonia	1		1			1	1
Unknowns	4	3	1			4	4

[a] Could not separate fetal atelectasis from neonatal atelectasis in all suspect cases.

Table 30

Summary of carcass utilization of 60[a] wolf-killed newborn caribou calves, Beverly calving ground, Northwest Territories, June 1983

User category	N	% with deep muscles missing	Utilization class % deep muscles utilized			% with viscera missing	Utilization class % viscera utilized			% with tongues missing	% with eye(s) missing
			All	Most	Some		All	Most	Some		
Wolves and gulls											
	35	88.6	25.7	42.9	20.0	100.0	88.6	11.4		85.7	82.9
Gulls only											
	24	41.7	4.2	20.8	16.7	58.3	37.5	8.3	12.5	87.5	75.0
Wolves or gulls											
	60[b]	68.3	16.7	33.3	18.3	83.3	68.3	10.0	5.0	85.0	78.3

[a] Two of the 62 wolf-killed calves were not used in the table because they were not fed on after they were killed.

[b] One calf carcass was fed on apparently only by a wolf (with only most of the viscera removed).

Table 31

Approximate estimate of utilization by predators or scavengers of 101 carcasses of caribou calves <1-week-old, Beverly calving ground, Northwest Territories, June 1983

Cause of death	Sample size[a]	No. fed on	% in utilization class[b]				
			1-9	10-34	35-49	50-69	70-90
Wolf-killed	62	60	22	38	22	12	6
Suspect wolf-killed	3	3		67		33	
Fetal atelectasis	5	2	100				
Neonatal atelectasis	2	1	100				
Suspect atelectasis	5	5		20	40	40	
Separation/malnutrition	8	5	100				
Patho-physiological	7	2	100				
Pneumonia	3	2	50	50			
Unknown	6	6		17	33	50	

[a] All calf carcasses included in 1983.

[b] Calculated for carcasses with deep muscle tissue or viscera missing by assuming: % util. = aver. whole wt. - carcass wt./aver. whole wt. (aver. whole wt. in 1983 = 5.42 kg). All 18 carcasses with only eye(s) or tongue missing were placed in the 1-9% utilization class regardless of carcass weight; and three carcasses that exceeded the mean weight (two wolf-kills, one separation/malnutrition) were also put in the 1-9% utilization class.

Table 32

Percentage distribution of utilization of caribou calf carcasses on an average weight[a] basis, Beverly calving ground, Northwest Territories, June 1983

	% utilization class				
Category	1-9[b]	10-34	35-49	50-69	70-90
Wolf predation (n=62[c])					
Wolf-killed calves fed on apparently by both wolves and scavenged by gulls (n=35)		43	26	20	11
Wolf-killed calves scavenged by gulls only (n=24)	54	29	17		
Wolf-killed calf fed on apparently by a wolf only (n=1)		100			
Suspected wolf predation (n=3)		67		33	
Cause(s) of death unknown (n=6)		17	33	50	
Non-predator causes (n=17[d])	64	12	12	12	

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[a] The average weight used in this calculation is the mean weight of the 23 whole carcasses found in June 1983 (Table 27:5.42 kg).

[b] All carcasses with only the tongue or eye(s) removed (or less than 0.25 kg of tissue) were placed in the 1-9% utilization class regardless of carcass weight.

[c] Two of the carcasses from wolf-killed calves were subsequently untouched by predators or scavengers.

[d] Total non-predator caused deaths equalled 30 but 13 carcasses in the non-predator category were untouched by scavengers after death.

Table 33

Distribution of ways by which wolves or gulls gained entries to body cavities or removed tongues and/or eye(s) when feeding on the carcasses of 60[a] wolf-killed caribou calves, Beverly calving ground, Northwest Territories, June 1983

% sample size for each combination	Points of entry (X)[b]					
	Rib cage	Abdomen	Flank	Mouth	Eye(s)	Anal area
Carcasses fed on apparently by both wolves and gulls (n=35[a])						
5.7	X	X	X	X	X	X
25.7	X	X	X	X	X	
2.9	X	X	X	X		X
2.9	X	X	X		X	X
2.9	X		X	X	X	X
5.7	X	X	X	X		
2.9	X	X	X		X	
11.4	X	X		X	X	
11.4	X		X	X	X	
2.9	X	X				X
2.9	X		X	X		
2.9	X	X				
2.9	X		X			
17.1 unknown[c]				X	X	
Carcasses fed on apparently by gulls only (n=24)						
16.6	X		X	X	X	
8.3			X	X	X	X
8.3	X		X	X		
4.2	X			X	X	
12.5			X	X	X	
8.3				X	X	X
8.3	X			X		
4.2	X			X	X	X
4.2			X		X	
12.5				X	X	
4.2				X		
4.2					X	
4.2						X
Carcass fed on apparently by wolf only (n=1)						
100.0	X					

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[a] Two wolf-killed calves were not subsequently fed on by predators or scavengers.

[b] (X) equals a point of entry: all (X's) in each row equal the combination of body entries for that percentage of carcasses.

[c] These six carcasses were too intensively utilized for us to determine the points of entry through the rib cage, abdomen, or flank.

Table 34

Distribution of caribou carcasses by whether or not any other animals were present when found, by death category, Beverly calving ground, Northwest Territories, June 1983

Death category by year	Gulls only	Maternal cow only	Gulls or maternal cows	Gulls and maternal cows	No other animals present	Total
Wolf-killed	14[a]	2	16[a]		46	62
Non-predator	9[a]	7	16	2	14	30
Suspect wolf-killed					3	3
Unknown	1	1			5	6
Adult cow	4[b]	4[b]			7	11

[a] Includes one carcass in each category with only an arctic fox present when found.
[b] Includes one carcass with a grizzly bear at it.

Table 35

A comparison of caribou calves who weighed less than or equal to or greater than 4.0 kg, by whether they died from atelectasis or some other cause, Beverly calving ground, Northwest Territories, 1981-83 (only calves with essentially whole body weights used).

Variable by category of death	Number by body weight (kg)		
	<4	≥4	Total
Observed			
atelectasis	7	16	23
others	2	50	52
O/E[a] index			
atelectasis	2.54	0.79	
others	0.32	1.09	
χ^2_1 values[b]			
atelectasis	6.55	0.89	7.44
others	2.89	0.37	3.26

[a] Observed/Expected

[b] P <0.01.

Table 36

Procedure for determining the most probable cause(s) of death of a calf whose carcass still contains the stomach and/or intestines with no milk present (evidence of malnutrition) and the lungs are missing.

Variables to be evaluated

(1) estimated age <1 d
(2) estimated age >1 <4 d
(3) estimated age <4 d
(4) never nursed - meconium still in intestines; stomach completely empty of solids and walls of stomach clean
(5) nursed - no meconium present; stomach with, at least, traces of vegetation present; and particles adhering to stomach walls
(6) never walked - Hoof class-1
(7) walked - Hoof classes -2 to -4
(8) pelage not completely cleaned by dam - remnants of afterbirth adhering to and patches of sticky amniotic fluids still on pelage
(9) pelage completely cleaned by dam

Evaluation of existing combination of the above conditions and the best subsequent diagnosis

Combination: 1 or 1 or 1 or 1
4 4 4 4
6 7 6 7
8 8 9 9

Diagnosis: 1st probability = suspect neonatal atelectasis
2nd probability = suspect separation or abandonment

Combination: 1 or 1 or 1 or 1 or 2 or 2 or 2 or 2 or 2
5 5 5 5 4 4 4 4 5
6 7 6 7 6 7 6 7 6
8 8 9 9 8 8 9 9 9

Diagnosis: equal probability = suspect neonatal atelectasis, or suspect separation or abandonment

Combination: 2
5
7
9

Diagnosis: 1st probability = suspect separation or abandonment
2nd probability = suspect neonatal atelectasis
3rd probability = suspect pneumonia

Table 36 (cont'd)

Combination:	3	or	3
	5		5
	6		7
	9		9

Diagnosis: 1st probability = suspect separation or abandonment
2nd probability = suspect pneumonia

Table 37

Sightings of wolves and grizzly bears during aerial surveys of the Beverly calving grounds, Northwest Territories, during 9 years between 1958 and 1982[a]

Years samples	Location relative to Thelon River	No. sightings		Literature source
		Wolves	Grizzly bears	
1958	north/south	6	2	Pruitt (1958)
1959	north/south	0	2	McEwen (1960)
1962	south	1	1	McEwen (1962)
1965	north	1	3	Look (1965)
1971	north/south	16[b]	0	Rippin (1971)
1974	north/south	50	0	R. Decker (pers. commun.)
1978	north	49	6	Heard and Decker (1980)
1980	north	13	4	Gunn and Decker (1982)
1982	north	6	1	Stephenson et al. (1983)

[a] Information from 1958 to 1980 taken from compilations by Fleck and Gunn (1982:Table 15 and Fig. 4).

[b] No wolves seen on northern segment of calving ground in 1971.

Table 38

A comparison of caribou calf carcasses from all wolf-killed versus all non-predator deaths by whether or not only gulls, or gulls or maternal cows (any other animals) were present at the carcasses when found, Beverly calving ground, Northwest Territories, May-June 1981

Variables by death category	Other animals present					
	Gulls only[a]			Gulls or maternal cows[b]		
	No	Yes	Total	No	Yes	Total
Observed						
wolf-killed	18	5	23	17	6	23
non-predator	25	7	32	20	12	32
O/E[c] index						
wolf-killed	1.00	1.00		1.10	0.80	
non-predator	1.00	1.00		0.93	1.15	
χ^2_1 values						
wolf-killed	-	-		0.15	0.30	0.45
non-predator	-	-		0.11	0.24	0.35

[a] $P = 1.00$.

[b] $P > 0.30$.

[c] O/E equals observed/expected index.

Table 39

A comparison of only those caribou calves found as singles or the first carcass in a clumped association for calf carcasses from wolf-killed versus non-predator deaths by whether or not only gulls, or gulls and maternal cows (any other animals) were present at the carcasses when found, Beverly calving ground, Northwest Territories, May-June 1981

Variables by death category	Other animals present					
	Gulls only[a]			Gulls or maternal cows[a]		
	No	Yes	Total	No	Yes	Total
Observed						
wolf-killed	12	5	17	11	6	17
non-predator	24	7	31	24	7	31
O/E[b] index						
wolf-killed	0.94	1.18		0.89	1.30	
non-predator	1.03	0.90		1.06	0.83	

[a] Neither set was statistically testable because in both sets the expected values for 'yes' cell for the wolf-killed calves were less than 5.00: 4.25 and 4.60, respectively.

[b] O/E equals observed/expected index.

Table 40

A comparison of caribou calf carcasses from all wolf-killed plus suspect wolf kills versus all non-predator deaths by whether or not only gulls, or gulls or maternal cows (any other animals) were present at the carcasses when found, Beverly calving ground, Northwest Territories, May-June 1981

Variables by death category	Other animals present					
	Gulls only[a]			Gulls or maternal cows[b]		
	No	Yes	Total	No	Yes	Total
Observed						
wolf-killed[c]	27	10	37	25	12	37
non-predator	25	7	32	20	12	32
O/E[d] index						
wolf-killed	0.97	1.10		1.04	0.93	
non-predator	1.04	0.89		0.96	1.08	
χ^2_1 values						
wolf-killed	0.03	0.09	0.12	0.04	0.06	0.10
non-predator	0.04	0.10	0.14	0.03	0.07	0.10

[a] $P > 0.50$.

[b] $P > 0.50$.

[c] Equals 23 wolf kills plus 14 suspect wolf kills.

[d] O/E equals observed/expected index.

Table 41

A comparison of only those caribou calves found as singles or the first carcass in a clumped association for calf carcasses from wolf-killed plus suspect wolf kills versus non-predator deaths by whether or not only gulls, or gulls and maternal cows (any other animals) were present at the carcasses when found, Beverly calving ground, Northwest Territories, May-June 1981

Varibles by death category	Other animals present					
	Gulls only[a]			Gulls or maternal cows[b]		
	No	Yes	Total	No	Yes	Total
Observed						
wolf-killed[c]	21	9	30	19	11	30
non-predator	24	7	31	19	12	31
O/E[d] index						
wolf-killed	0.95	1.14		1.02	0.97	
non-predator	1.05	0.86		0.98	1.03	
χ^2_1 values						
wolf-killed	0.06	0.15	0.21	0.01	0.01	0.02
non-predator	0.06	0.16	0.22	0.01	0.01	0.02

[a] $P > 0.50$.

[b] $P > 0.80$.

[c] Equals 17 wolf kills plus 13 suspect wolf kills.

[d] O/E equals observed/expected index.

Table 42

A comparison of caribou calf carcasses from all wolf-killed versus all non-predator deaths by whether or not only gulls, or gulls or maternal cows (any other animals) were present at the carcasses when found, Beverly calving ground, Northwest Territories, June 1982

Variables by death category	Other animals present					
	Gulls only[a]			Gulls or maternal cows[b]		
	No	Yes	Total	No	Yes	Total
Observed						
wolf-killed	43	26	69	42	27	69
non-predator	17	4	21	8	13	21
O/E[c] index						
wolf-killed	0.93	1.13		1.10	0.88	
non-predator	1.21	0.57		0.69	1.39	
χ^2_1 values						
wolf-killed	0.23	0.39	0.62	0.38	0.44	0.82
non-predator	0.62	1.29	1.91	1.12	1.42	2.54

[a] $P > 0.10$.
[b] $P > 0.05$.
[c] O/E equals observed/expected index.

Table 43

A comparison of only those caribou calves found as singles or the first carcass in a clumped association for calf carcasses from wolf-killed versus non-predator deaths by whether or not only gulls, or gulls and maternal cows (any other animals) were present at the carcasses when found, Beverly calving ground, Northwest Territories, June 1982

Variables by death category	Other animals present					
	Gulls only[a]			Gulls or maternal cows[b]		
	No	Yes	Total	No	Yes	Total
Observed						
wolf-killed	11	11	22	11	11	22
non-predator	11	1	12	4	8	12
O/E[c] index						
wolf-killed	0.77	1.42		1.13	0.90	
non-predator	1.42	0.24		0.76	1.19	
χ^2_1 values						
wolf-killed				0.16	0.12	0.28
non-predator				0.30	0.24	0.54

[a] Not testable.

[b] $P > 0.30$.

[c] O/E equals observed/expected index.

Table 44

A comparison of caribou calf carcasses from all wolf-killed versus all non-predator deaths by whether or not only gulls, or gulls or maternal cows (any other animals) were present at the carcasses when found, Beverly calving ground, Northwest Territories, June 1983

Variables by death category	Other animals present					
	Gulls only[a]			Gulls or maternal cows[b]		
	No	Yes	Total	No	Yes	Total
Observed						
wolf-killed	48	14[c]	62	46	16[c]	62
non-predator	21	9	30	14	16	30
O/E[d] index						
wolf-killed	1.03	0.90		1.14	0.74	
non-predator	0.93	1.20		0.72	1.53	
χ^2_1 values						
wolf-killed	0.04	0.16	0.20	0.79	1.46	2.25
non-predator	0.11	0.30	0.41	1.53	2.93	4.46

[a] $P > 0.30$.

[b] $P < 0.01$.

[c] Includes one carcass with only an Arctic fox on it when found.

[d] O/E equals observed/expected index.

Table 45

A comparison of only those caribou calves found as singles or the first carcass in a clumped association for calf carcasses from wolf-killed versus non-predator deaths by whether or not only gulls, or gulls and maternal cows (any other animals) were present at the carcasses when found, Beverly calving ground, Northwest Territories, June 1983

Variables by death category	Other animals present					
	Gulls only[a]			Gulls or maternal cows[b]		
	No	Yes	Total	No	Yes	Total
Observed						
wolf-killed	22	8[c]	30	22	8[c]	30
non-predator	15	8	23	9	14	23
O/E[d] index						
wolf-killed	1.05	0.88		1.25	0.64	
non-predator	0.93	1.15		0.67	1.47	
χ^2_1 values						
wolf-killed	0.05	0.13	0.18	1.10	1.61	2.71
non-predator	0.08	0.16	0.24	1.46	2.11	3.57

[a] $P > 0.50$.

[b] $P < 0.02$.

[c] Includes one carcass with only an Arctic fox on it when found.

[d] O/E equals observed/expected index.

Table 46

A comparison of those calves that were scavenged to those that were not, by whether or not the maternal cow was present when its calf was found (maternal cow remained with her dead calf), Beverly calving ground, Northwest Territories, 1981-83

Variable by presence of maternal cow	Carcass scavenged[a] No	Carcass scavenged[a] Yes	Total
Observed			
cow present	14	11	25[b]
no	26	203	229
O/E[c] index			
cow present	3.55	0.52	
no	0.72	1.05	
χ^2 value			
cow present	25.62	4.85	30.47
no	2.83	0.48	3.31

[a] $P < 0.001$.

[b] Two calves that were found alive and one that was observed delivered dead were deleted from this consideration.

[c] O/E equals observed/expected index.

Table 47

A comparison of those calves found with their maternal cows still present to those without their maternal cows present, by whether or not the calf died from predation or a non-predator cause, Beverly calving ground, Northwest Territories, June 1981-83

Variable by death category	Maternal cow present[a]		Total
	No	Yes	
Observed			
wolf-killed	167[b]	7	174
non-predator	62	18	80
O/E[c] index			
wolf-killed	1.06	0.41	
non-predator	0.86	2.29	
χ^2 value			
wolf-killed	0.56	5.96	6.52
non-predator	1.41	13.10	14.51

[a] $P < 0.001$.

[b] Includes one grizzly bear-killed calf.

[c] O/E equals observed/expected index.

Table 48

A comparison of only those calves that died from non-predator causes that were scavenged to those that died from non-predator causes and were not scavenged, by whether or not the maternal cow was present when its calf was found (maternal cow remained with her dead calf), Beverly calving ground, Northwest Territories, 1981-83

Variable by presence of maternal cow	Carcass scavenged[a]		
	No	Yes	Total
Observed			
cow present	14	4	18[b]
no	18	44	62
O/E[c] index			
cow present	7.20	10.80	
no	24.80	37.20	
χ^2 value			
cow present	6.36	4.29	10.65
no	1.81	1.20	3.01

[a] $P < 0.001$.

[b] Two calves that were found alive and one that was observed delivered dead were deleted from this consideration.

[c] O/E equals observed/expected index.

Table 49

Conditions used and calculations made in assessing theoretical 'renewable value' of 1000 female caribou calves or 1000 (3+ yr-old) female caribou (and all their subsequent generations of female offspring in both cases) removed annually from the Beverly herd over a 50-yr-period

Condition	
Code	Condition
(1.)	Assumed secondary sex ratio of calves equals 52 males::48 females
(2.)	Each annual cohort survives 16 yr 0-1, 1-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10, 10-11, 11-12, 12-13, 13-14, 14-15, and 15-16
(3.)	Survival rates (%)[a]
(3a.)	Low estimate - calf survival to 1-yr equals 40%
(3b.)	High estimate - calf survival to 1-yr equals 66%
(4.)	Survival rates for all estimates are the same after the first year (%) 70.0, 2nd yr; 93.3, 3rd yr; 92.9, 4th yr; 92.3, 5th yr; 91.7, 6th yr; 90.9, 7th yr; 88.9, 8th yr; 87.5, 9th yr; 85.7, 10th yr; 83.3, 11th yr; 79.9, 12th yr; 74.7, 13th yr; 66.1, 14th yr; 48.7, 15th yr; and 0.0, 16 yr
(5.)	Reproductive rates (%) - the same for all estimates[b]
(5a.)	0, 1st yr; 2, 2nd yr; 48, 3rd yr; 82, 4th yr; 79, 5th-15th yr; and 0, 16th yr
(5b.)	0, 1st yr; 2, 2nd yr; 48, 3rd yr; 82, 4th yr; 89, 5th-15th yr; and 0, 16th yr

Table 49 cont.

Specific condition for estimates

a. Conditions (1.), (2.), and (4.) are common to all four estimates for calves and all four estimates for adult cows (see above)

b. Low estimate for calves (A) and low estimate for adult cows (B) based on specific conditions (3a.) and (5a.)

c. Low-middle estimate for calves (C) and low-middle estimate for adult cows (D) based on specific conditions (3a.) and (5b.)

d. High-middle estimate for calves (E) and high-middle estimate for adult cows (F) based on specific conditions (3b.) and (5a.)

e. High estimate for calves (G) and high estimate for adult cows (H) based on specific conditions (3b.) and (5b.)

Step number	Calculations made for estimates
1.	The subsequent annual production of female calves by the original 1000 female calves or the original 1000 adult female caribou was generated by computer for a 50-yr-period, using the statistics listed above. Then the annual number of female calves produced for each of the four combinations of original calves or four combinations of original adult cows was summed for a 50-yr-period (Item no. 1, App. 24, Table 1)
2.	The annual number of female calves produced by subsequent annual cohorts of 1000 female calves or 1000 adult cows over the remainder of the 50-yr-period was obtained by subtracting one year's production, starting with the 50th year and working in descending order of years, one year at a time. The resultant values for each of the 50 yr were then summed to get the production that theoretically would have been realized by the 50 annual cohorts of 1000 female calves or 1000 adult cows each over the 50-yr-period (Item no. 2, App. 24, Table 1)

Table 49 cont.

Step number	Calculations made for estimates
3.	The summations of female calves produced for female calves or adult cows were then divided by 0.48 (the proportion of female calves produced annually) to obtain the total production of calves (females + males) over the 50-yr-period (Item no. 3, App. 24, Table 1)
4.	The various productions of calves were then multiplied by 0.261 (low survival to 1st year of life - estimates A, B, C, and D) or 0.431 (high survival to the 1st year of life - high estimates E, F, G, and H) to get average number of 3-yr-old caribou over a 50-yr-period (the proportion of calves surviving on the average to their 3rd year of life (0.40x0.70x0.933 - low estimates A and B, and low-middle estimates C and D) or (0.66x0.70x0.933 - high-middle estimates E and F, and high estimates G and H) (Item no. 4, App. 24, Table 1)
5.	The product from each estimate was then divided by 50 (yr) to get the average annual number of 3-yr-old caribou (Item no. 5, App. 24, Table 1). The results suggest that 660, 784, 3405, or 4347 3-yr-old caribou would be lost annually over a 50-yr-period due only to the annual loss of 1000 female calves; and that 2779, 3361, 9211, or 12 101 3-yr-old caribou would be lost annually over a 50-yr-period due only to the annual loss of 1000 adult cows
6.	If the replacement value of those caribou was $936/carcass, the annual replacement costs would range between $617 760 and $11 326 536 (Item no. 6, App. 24, Table 1)
7.	If the replacement value of those caribou doubled in the near future (± 20 yr) the annual replacement costs would range between about $1 200 000 and $22 000 000

Table 49 cont.

Table 1

Calculation of estimates and costs

Starting with calves				Starting with adult cows			
A	C	E	G	B	D	F	H
Item 1. Summation of original 1,000 plus all of their subsequent female offspring							
2038	2569	9379	13 156	7856	10 089	23 890	34 754
Item 2. Summation of 50 yr (summation of all female cohorts over 50 yr)							
60 694	72 177	189 659	242 093	255 594	309 139	512 934	673 872
Item 3. (Item 2.) divided by (0.48) - 52 males::48 females							
126 446	150 370	395 123	504 360	532 489	644 041	1 068 613	1 403 901
Item 4. (Item 3.) x (0.261) = survival to 3rd year of life (0.40x0.70x0.933) for estimates A, C, E, and G and (Item 3) x (0.431) = survival to 3rd year of life (0.66x0.70x0.933) for estimates B, D, G, and H							
33 002	39 246	170 298	217 379	138 979	168 094	460 572	605 081
Item 5. (Item 4.) divided by 50 yr							
660	784	3405	4347	2779	3361	9211	12 101
Item 6. (Item 5.) x ($936) = replacement costs (in 1985 dollars)							
$617 760	$733 824	$3 187 080	$4 068 792	$2 601 144	$3 145 896	$8 621 496	$11 326 536

---

[a] Assumed constant proportional annual calf loss each year as average approximation of what might be happening in the wild.

[b] Used relatively low rate of reproduction (79%) to obtain conservative estimates.

Table 50

Causes of death of Russian domestic reindeer calves (1934-54) in the first month of life on tundra and taiga calving areas (taken from Baskin 1983:Table 2)

	% mortality	
Cause of death	Tundra (n = 4797)	Taiga (n = 4926)
(1) Teratogensis	3.2	2.1
(2) Born weak	21.7	10.0
(3) Abandoned	16.6	18.0
(4) Mothers without milk	2.4	1.5
(5) Trampled by mothers	1.2	1.4
(6) Drowned	1.3	2.7
(7) Frozen during blizzards	12.8	6.4
(8) Killed by predators	4.2	12.2
(9) Killed by dogs	1.2	0.8
(10) Died of diseases	21.3	29.6
(11) Broken legs	1.6	3.9
(12) Lost (cause of death unknown)	12.5	11.3

Table 51

A comparison of the major categories of calf mortalities between Beverly caribou herd on a tundra calving ground (1981-83) in central mainland, NWT, Canada and Russian domestic reindeer (1934-54) on tundra and on taiga calving areas (data taken from Baskin 1983:Table 2), based on average percentages of deaths over time periods

Cause of death	Beverly caribou		Russian reindeer	
	% (n = 225)[a]	% (n = 257)[b]	% tundra (n = 4197)[c]	% taiga (n = 4369)[c]
Predation	68.9	67.8	6.2	14.7
Atelectasis	14.2	17.5	24.8	11.3
Separation/malnutrition	6.2	5.4	19.0	20.3
Patho-physiological	6.7	5.8	50.0	53.7
Pneumonia	4.0	3.5	0.0	0.0

[a] Only those calves for which positive determinations were made (minus suspect cases and unknowns).
[b] Minus unknowns only (suspect cases included).
[c] Minus unknowns: 600 from tundra (n = 4797); and 557 from taiga (n = 4926).

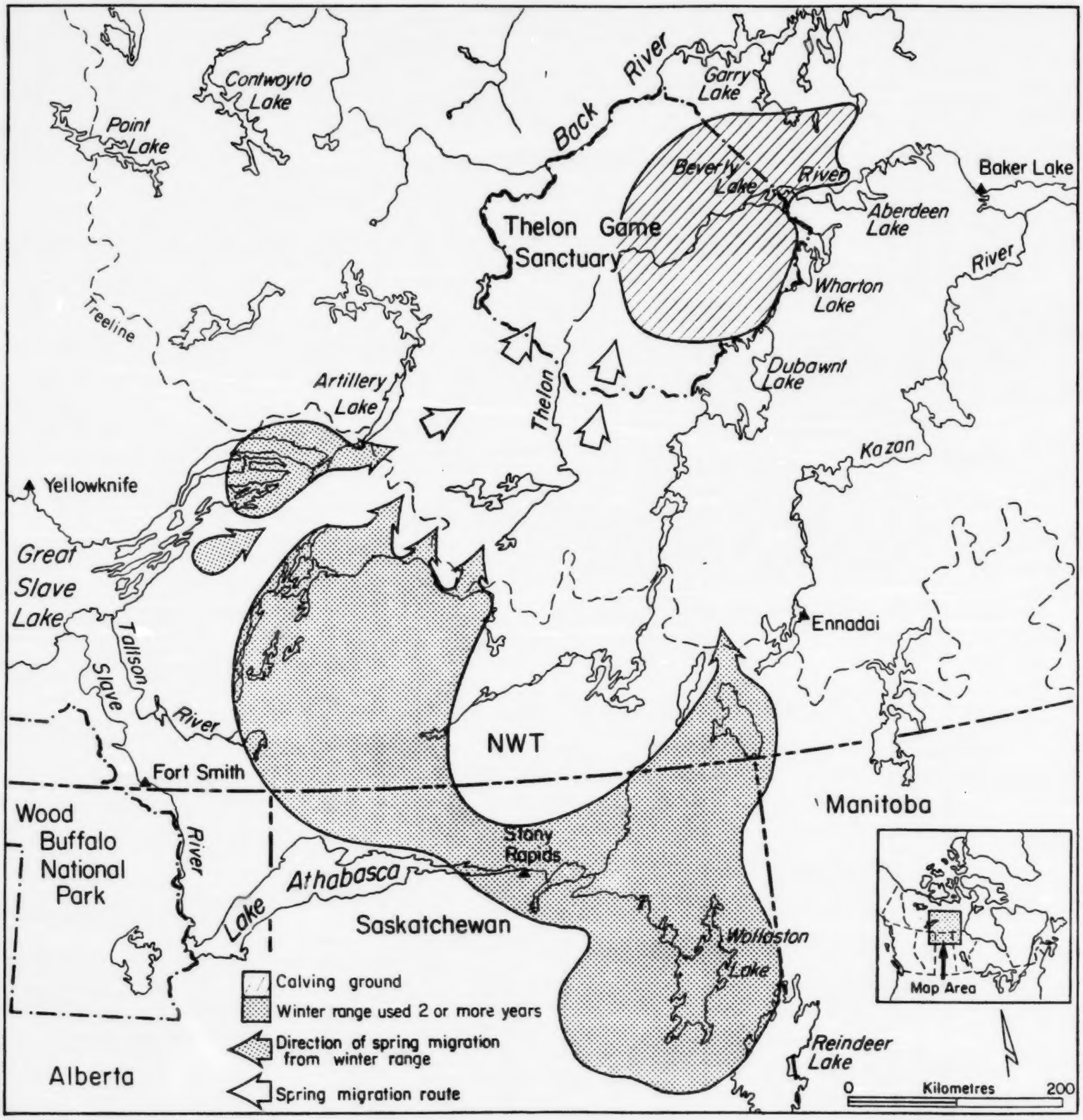
Contwoyto Lake
Point Lake
Back River
Garry Lake
Beverly Lake
River
Baker Lake
Aberdeen Lake
Thelon Game Sanctuary
Wharton Lake
River
Treeline
Dubawnt Lake
Artillery Lake
Thelon
Kazan
Yellowknife
Great Slave Lake
Taltson
Slave
River
Ennadai
NWT
Fort Smith
Manitoba
Wood Buffalo National Park
River
Stony Rapids
Lake Athabasca
Saskatchewan
Wollaston Lake
Calving ground
Winter range used 2 or more years
Direction of spring migration from winter range
Spring migration route
Reindeer Lake
Alberta
0 Kilometres 200
Map Area

Figure 1. Known winter range, direction of spring migration, and calving grounds of the Beverly barren-ground caribou herd, 1950-79 (after Fleck and Gunn 1982:Fig. 3) and this report 1981-83

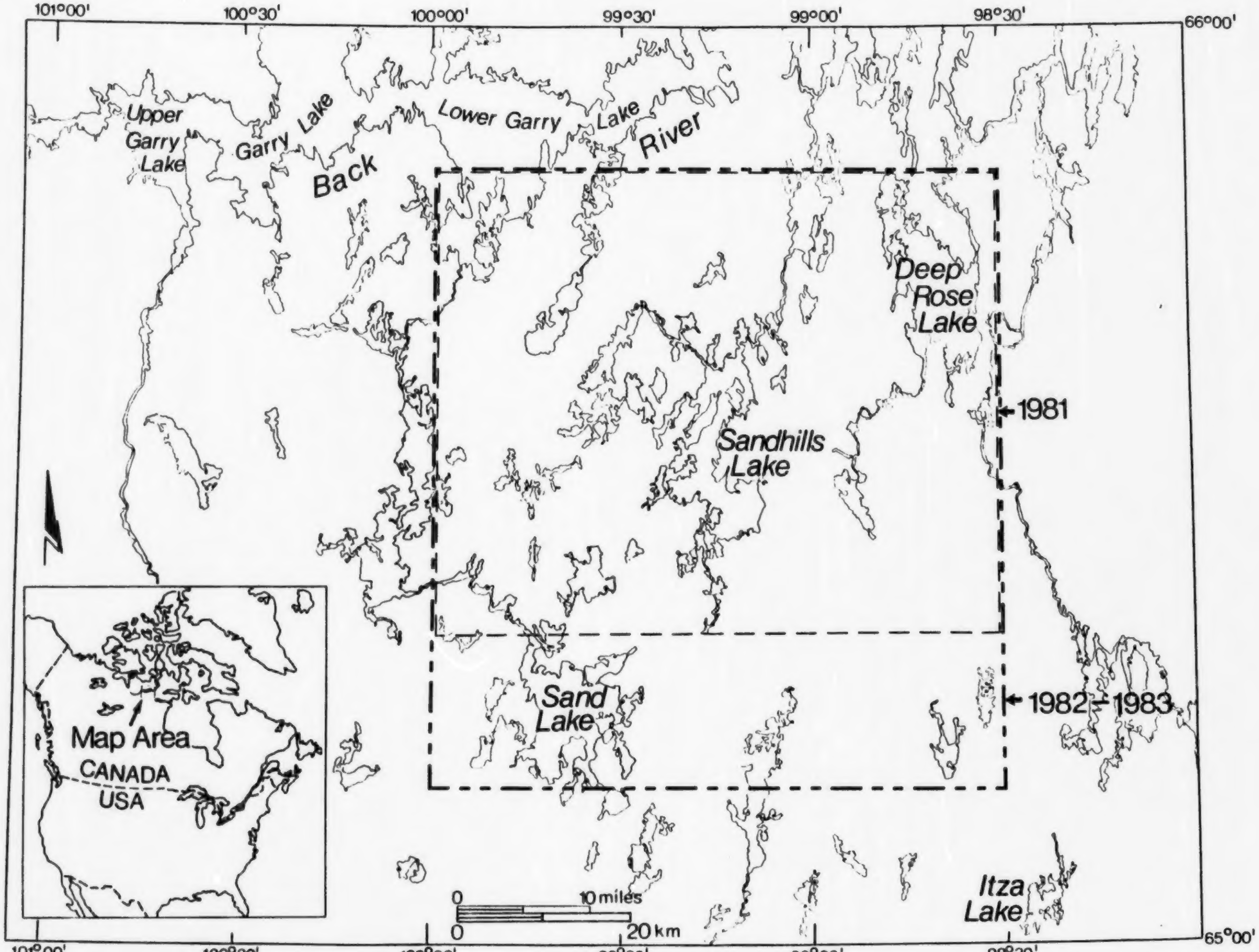
101°00'
100°30'
100°00'
99°30'
99°00'
98°30'
66°00'
65°00'
Upper Garry Lake
Garry Lake
Back
Lower Garry Lake
River
Deep Rose Lake
Sandhills Lake
Sand Lake
Itza Lake
1981
1982 – 1983
Map Area
CANADA
USA
0
10 miles
0
20 km

Figure 2. Areas searched by helicopter for dead caribou in May-June 1981, June 1982, and June 1983, Beverly calving ground, Northwest Territories

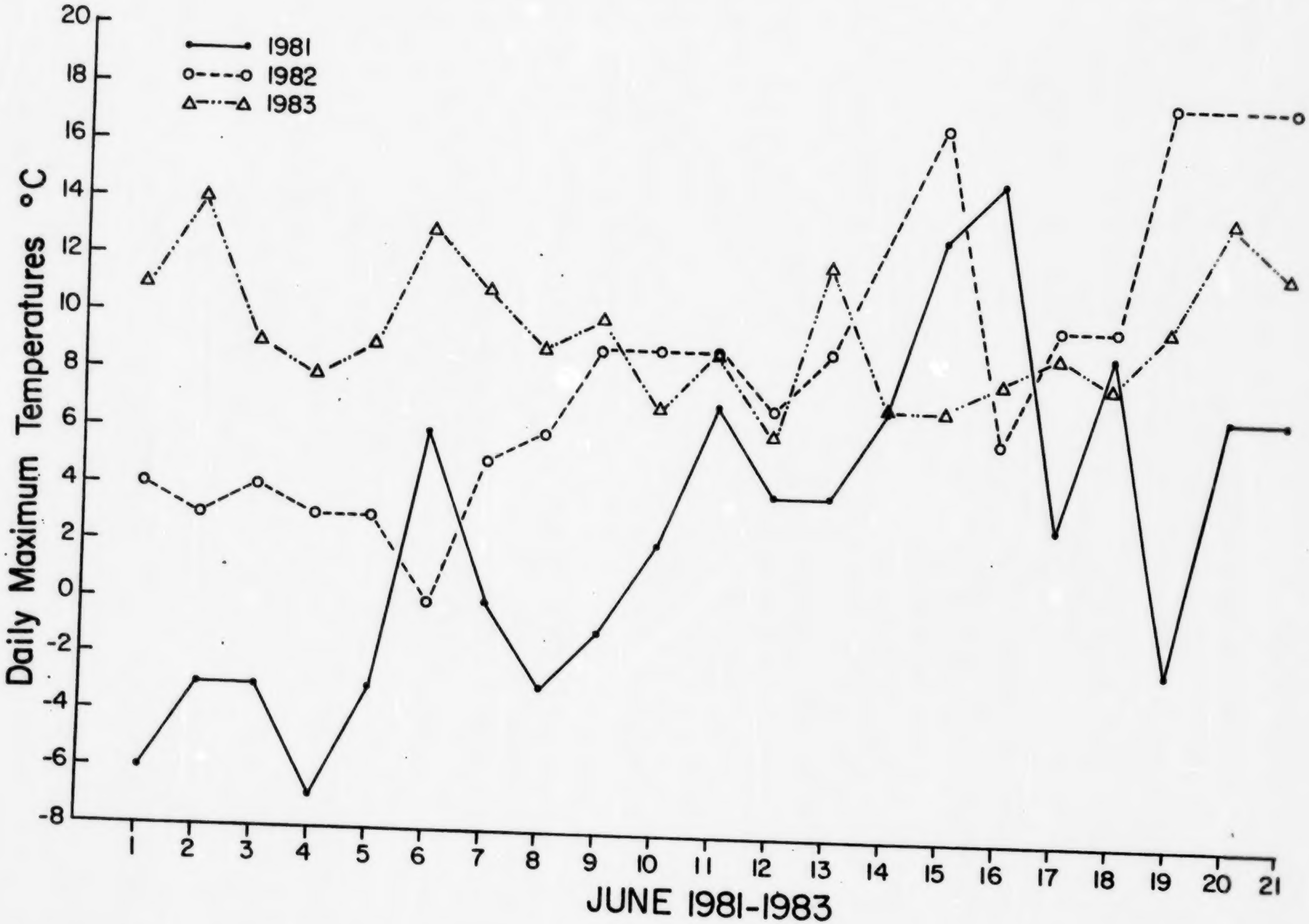

Figure 3. Daily maximum temperatures taken at the Itza Lake base camp, Northwest Territories, June 1981-83

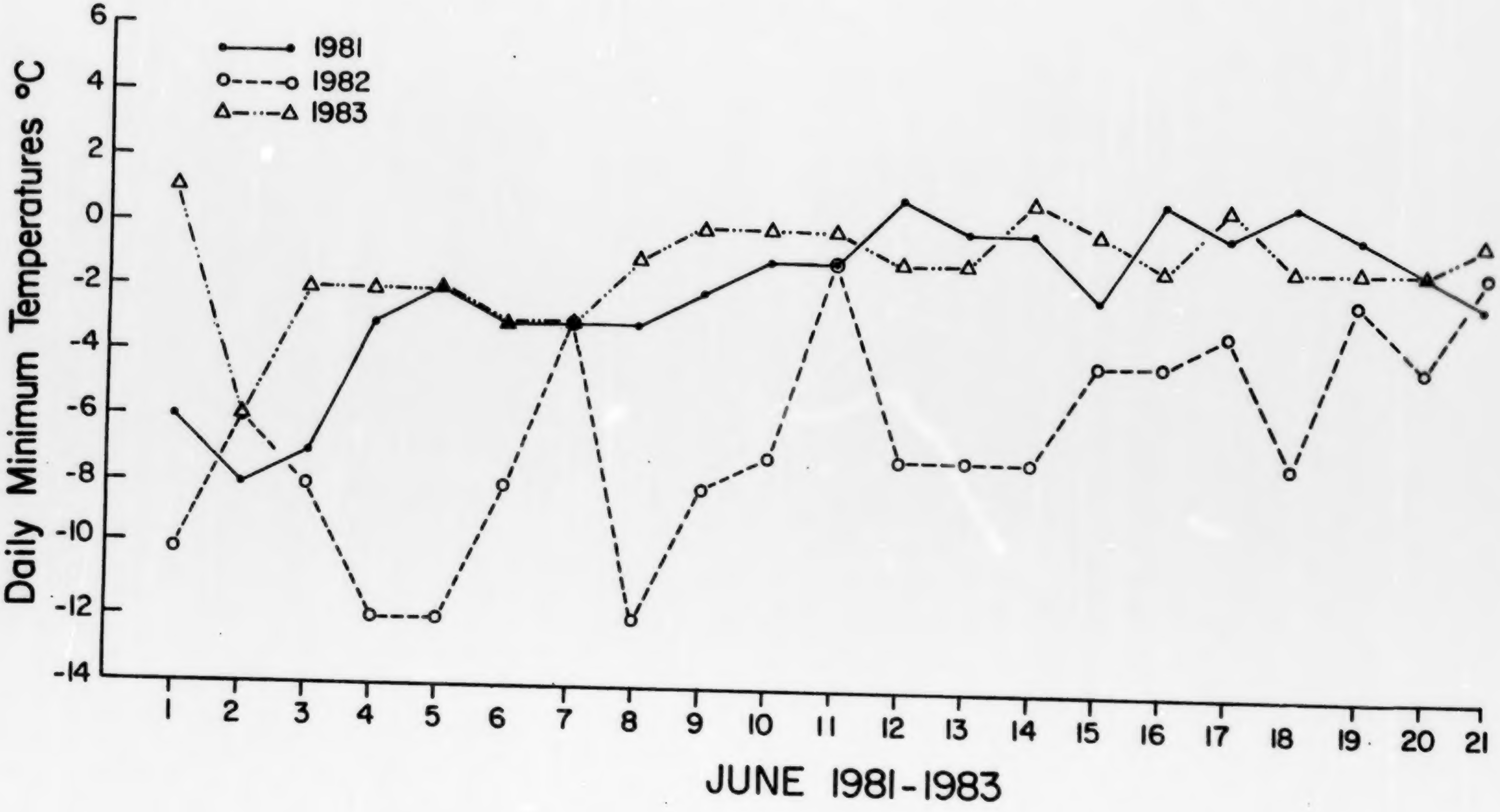

Figure 4. Daily minimum temperatures taken at the Itza Lake base camp, Northwest Territories, June 1981-83

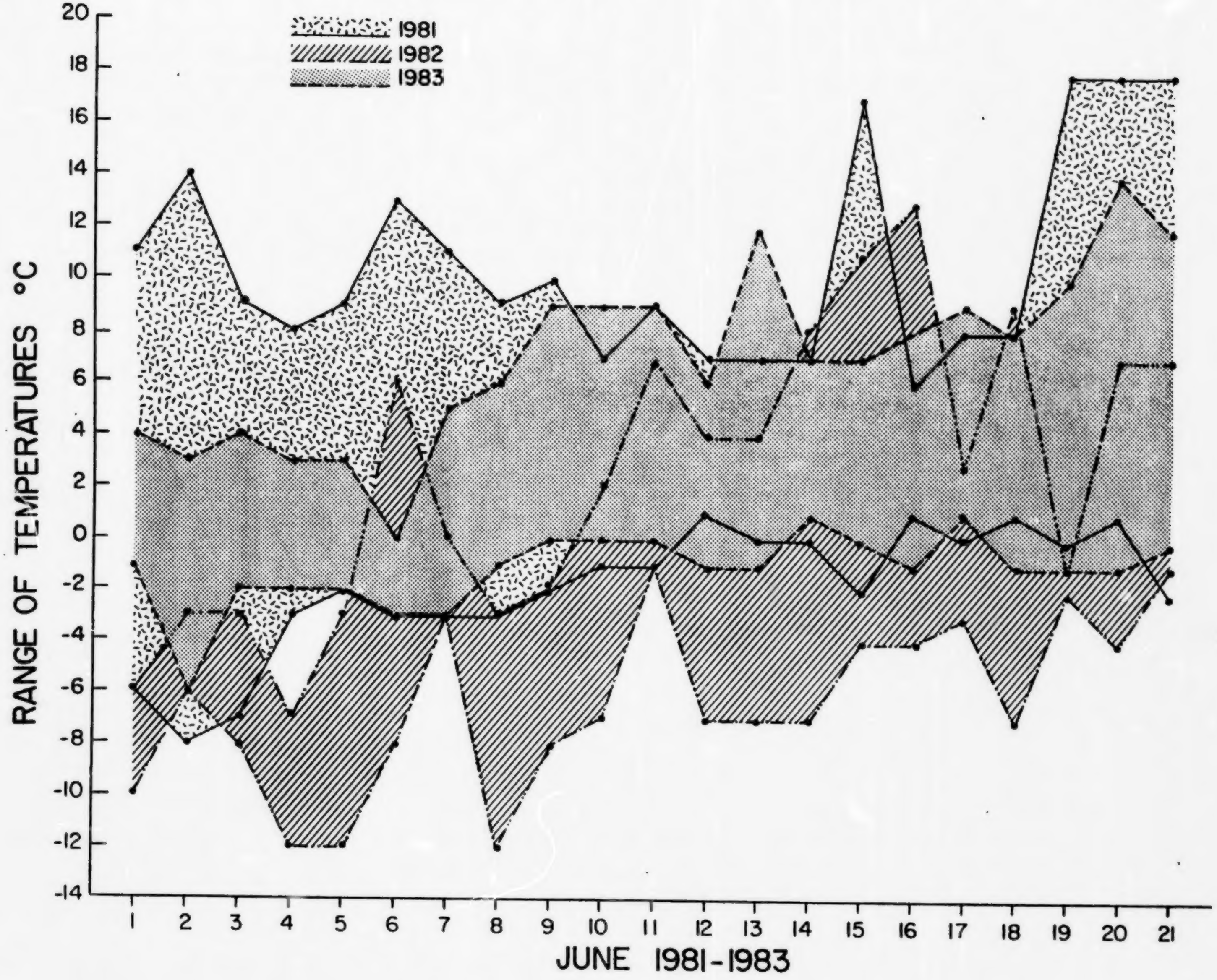

Figure 5. Range of temperatures experienced at the Itza Lake base camp, Northwest Territories, June 1981-83

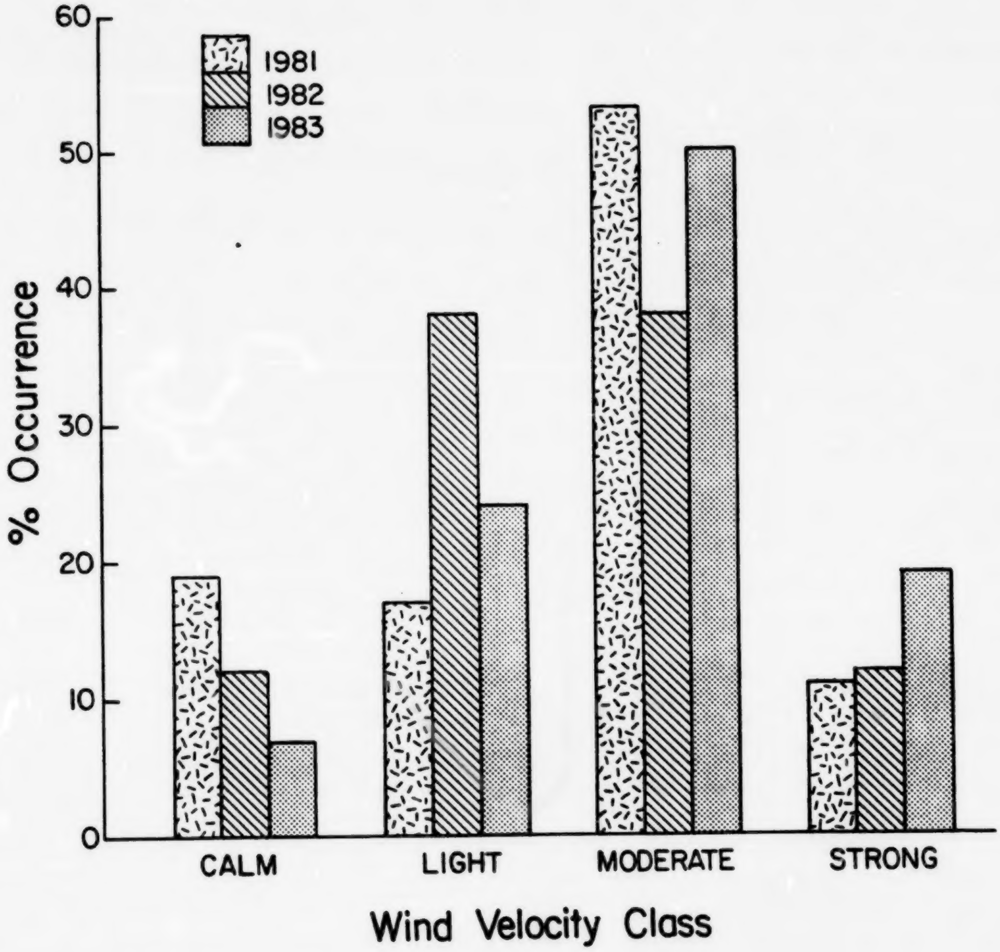

Figure 6. Frequency of occurrence of wind velocity classes at the Itza Lake base camp, Northwest Territories, June 1981-83

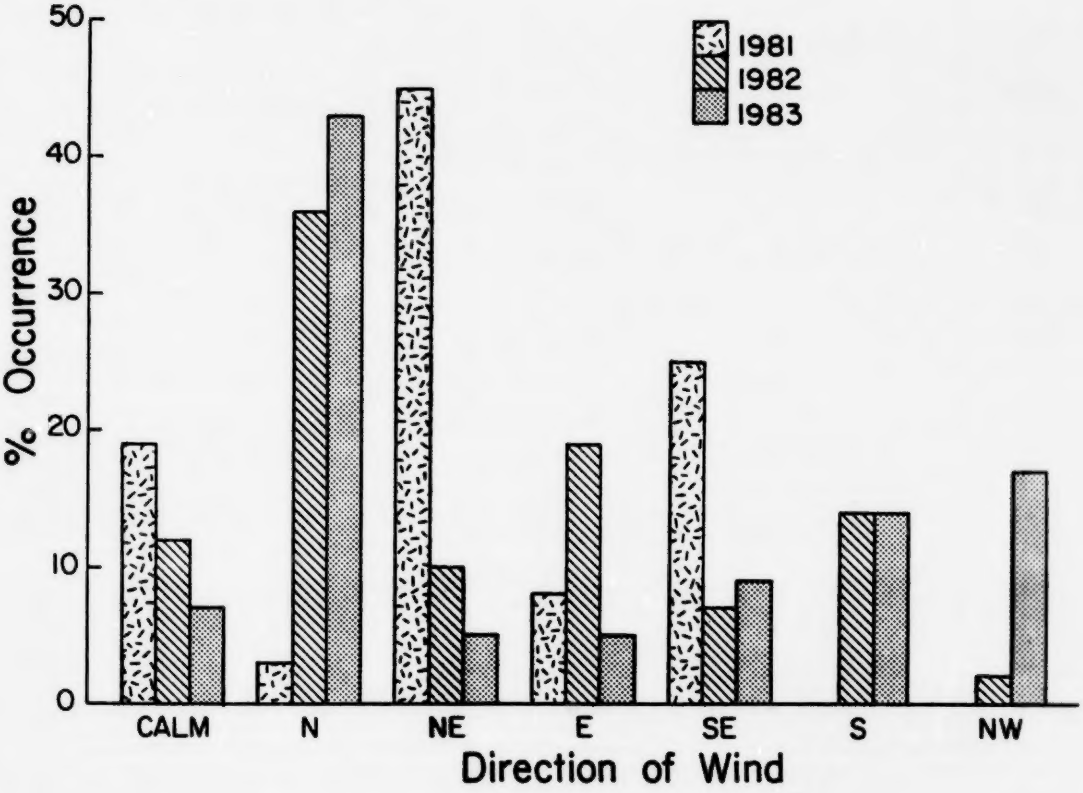

Figure 7. Frequency of occurrence of wind direction at the Itza Lake base camp, Northwest Territories, June 1981-83

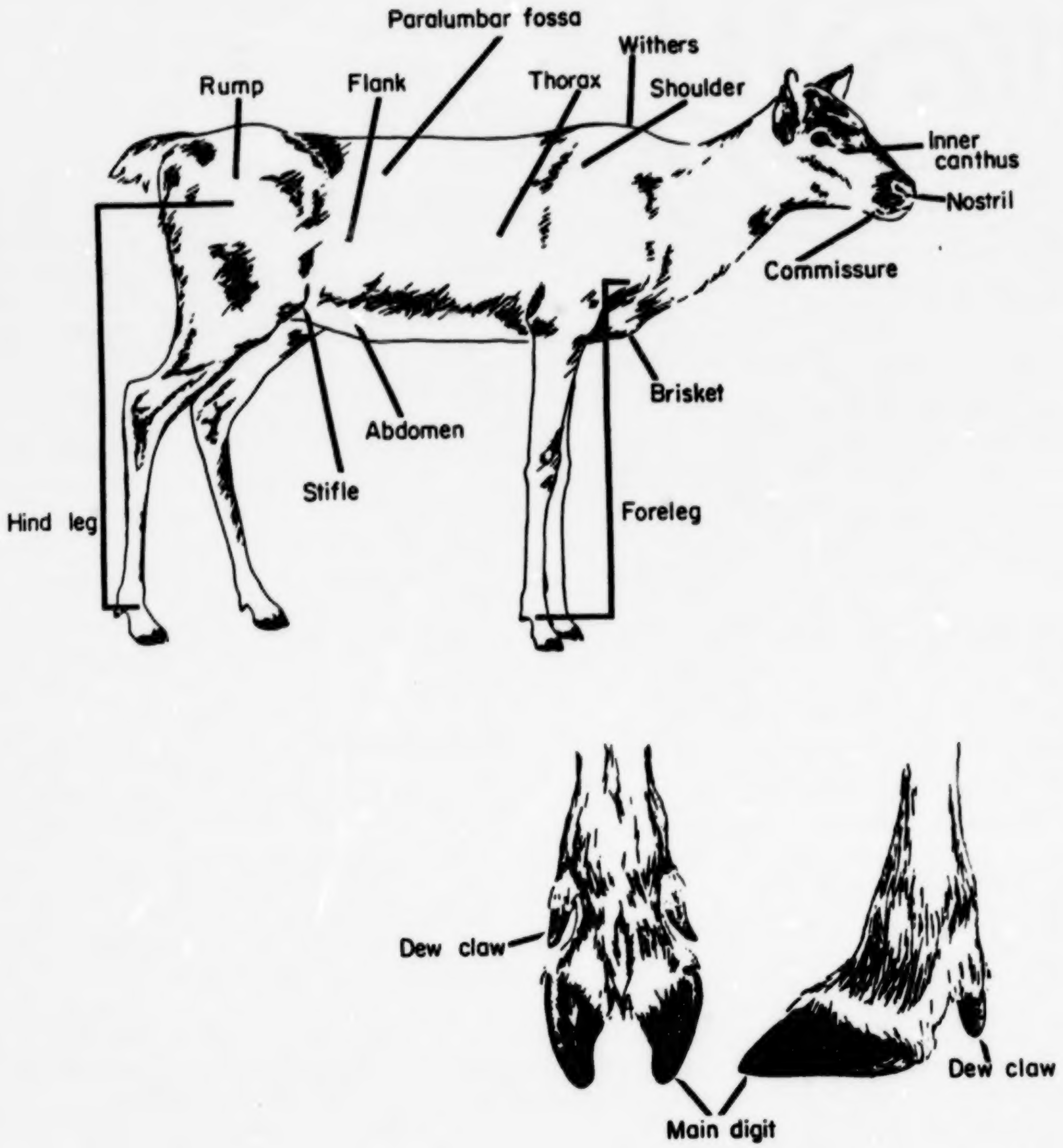
Paralumbar fossa
Withers
Rump
Flank
Thorax
Shoulder
Inner canthus
Nostril
Commissure
Brisket
Abdomen
Stifle
Hind leg
Foreleg
Dew claw
Dew claw
Main digit

Figure 8. External structures of the caribou used as reference points in necropsy case histories

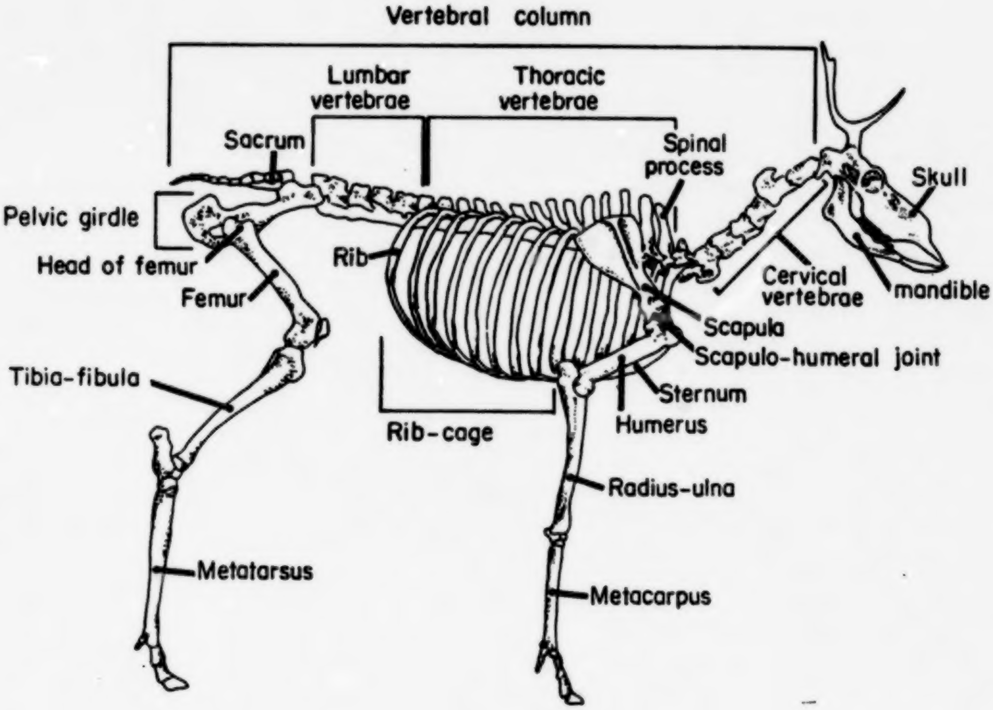
Vertebral column
Lumbar vertebrae
Thoracic vertebrae
Sacrum
Spinal process
Skull
Pelvic girdle
Head of femur
Rib
Femur
Cervical vertebrae
mandible
Scapula
Scapulo-humeral joint
Tibia-fibula
Sternum
Rib-cage
Humerus
Radius-ulna
Metatarsus
Metacarpus

Figure 9. Skeletal parts of the caribou used as reference points in necropsy case histories

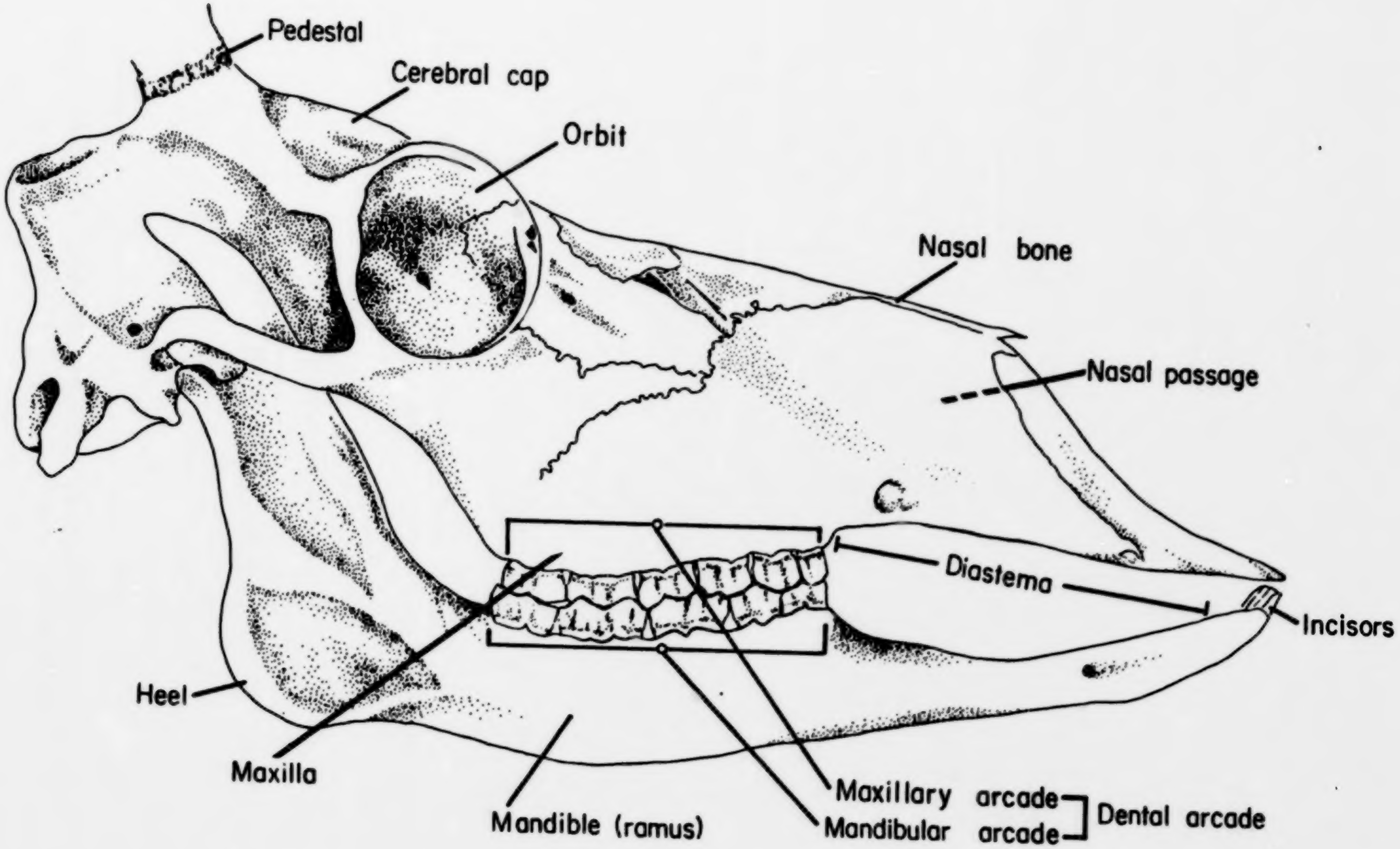
Pedestal
Cerebral cap
Orbit
Nasal bone
Nasal passage
Diastema
Incisors
Heel
Maxilla
Mandible (ramus)
Maxillary arcade
Mandibular arcade
Dental arcade

Figure 10. Parts of the skull of the caribou used as reference points in necropsy case histories

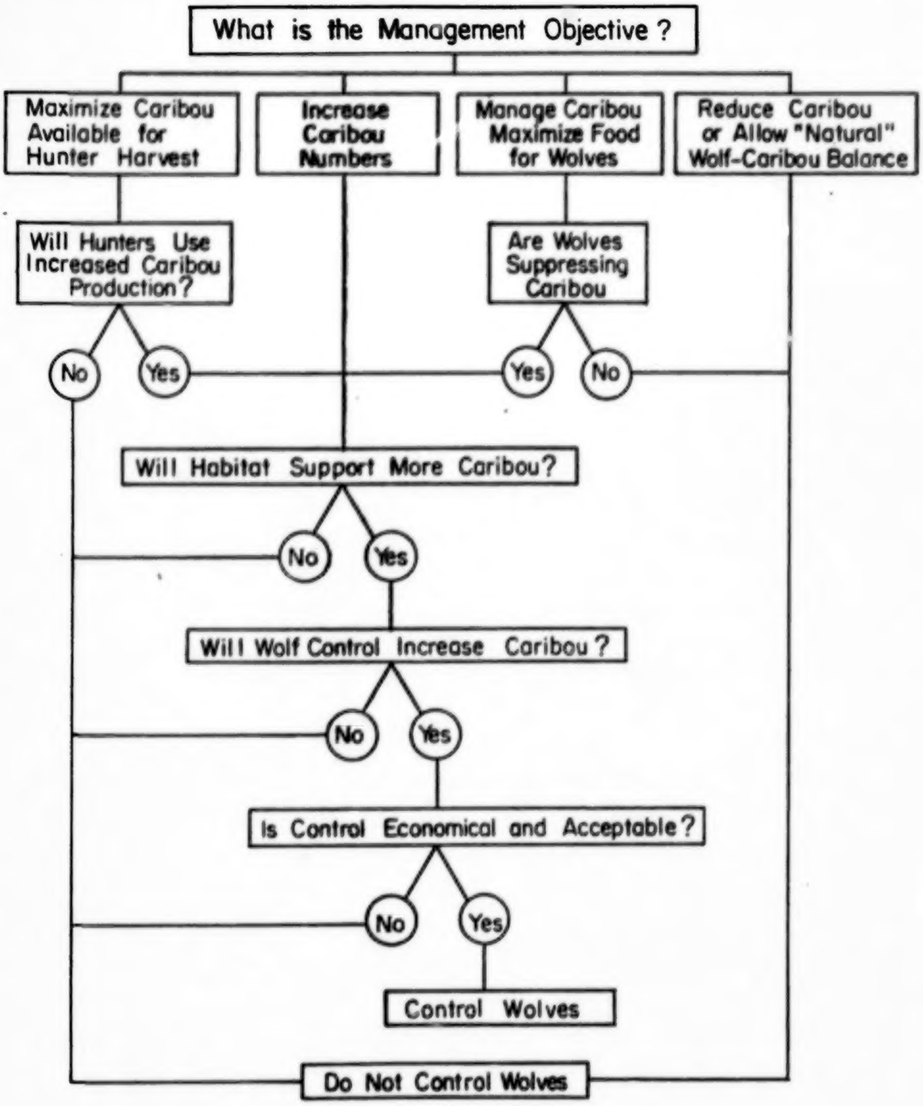
What is the Management Objective ?
Maximize Caribou Available for Hunter Harvest
Increase Caribou Numbers
Manage Caribou Maximize Food for Wolves
Reduce Caribou or Allow "Natural" Wolf-Caribou Balance
Will Hunters Use Increased Caribou Production?
Are Wolves Suppressing Caribou
No
Yes
Yes
No
Will Habitat Support More Caribou?
No
Yes
Will Wolf Control Increase Caribou ?
No
Yes
Is Control Economical and Acceptable?
No
Yes
Control Wolves
Do Not Control Wolves

Figure 11. Proposed logic for the use of wolf control in caribou management (after Connolly 1978)

Appendix 1

Daily maximum and minimum temperatures recorded at "Itza Lake" base camp, Beverly calving ground, Northwest Territories, May-June 1981-83

Day of year	Temperatures °C					
	1981		1982		1983	
	Max.	Min.	Max.	Min.	Max.	Min.
28/5	-	-2	-	-	12	-
29	2	-6	-	-	12	-3
30	11	-12	-	-	6	-2
31	14	-12	-5	-9	5	-2
1/6	11	-6	-6	-10	4	-1
2	14	-8	-3	-6	3	-6
3	9	-7	-3	-8	4	-2
4	8	-3	-7	-12	3	-2
5	9	-2	-3	-12	3	-2
6	13	-3	6	-8	0	-3
7	11	-3	0	-3	5	-3
8	9	-3	-3	-12	6	-1
9	10[a]	-2	-1	-8	9	0
10	7	-1	2	-7	9	0
11	9	-1	7	-1	9	0
12	7	1	4	-7	6	-1
13	9	0	4	-7	12	-1
14	7[a]	0	8	-7	7	1
15	17	-2	11	-4	7	0
16	6	1	13	-4	8	-1
17	10	0	3	-3	9	1
18	10	1	9	-7	8	-1
19	18	0	-2	-2	10	-1
20	-	-1	7	-4	14	-1
21	18	-2	7	-1	12	0
22	9	0	1	0	-	1
23	16	1	7	-6	-	-
24	18[a]	2	3	-6	-	-
25	18[a]	0	6	-4	-	-
26	-	-	3	-1	-	-
27	-	-	10	-4	-	-
28	-	-	14	1	-	-
29	-	-	17	1	-	-
30	-	-	-	3	-	-

[a] Estimated - based on relative physical impression in relation to last actual reading.

Appendix 2

Key to determining carcass 'utilization class' for deep muscle tissue taken from dead caribou calves, Beverly calving ground, Northwest Territories, 1981-83

Utilization class	Deep muscle tissue (X[a])		
	Hindquarters	Forequarters	Rump
All	X	X	X
Most	X	X	
	X	P	X
	P	P	X
	X	P	
	P	P	P
Some	P	P	
	X		
		X	
	P		
		P	
			P
None	-	-	-

---

[a] X equals muscle masses essentially all removed; P equals some or all muscle masses only partially gone.

Appendix 3

Key to determining carcass 'utilization class' for viscera taken from dead caribou calves, Beverly calving ground, Northwest Territories, 1981-83

Utilization class	Viscera (X^a)						
	Lungs	Heart	Liver	Stomach	Milk curds	Kidneys	Intestinal track
All	X	X	X	X	X	X	X
Most	P	X	X	X	X	X	X
	P	X	X	X	X	P	P
	X	X	X	X	X		X
	P		X	X	X	X	X
	X	X	P	X	X		P
	X	X	X	X	X		
			X	X	X	X	X
			P	X	X	X	X
			X	X	X	P	P
				X	X	X	X
Some		X		X	X		
					X	X	X
			P	X			X
	X	X					
				X	X		
	P	X					
				X			X
						X	P
						X	
	P						
							P
None	–	–	–	–	–	–	–

[a] X equals organ or part totally missing; P equals organ or part only partially gone.

Appendix 4

A glossary of working definitions for terms (mostly biological) used in this report (all underlined words are defined in this glossary).

'abdomen (abdomens)' --
the belly which is the region of the body lying between the diaphragm and the pelvis (see Fig. 8).

'abdominal area (abdominal areas)' --
an area on or in the abdomen.

'abdominal cavity (abdominal cavities)' --
the largest of the body cavities, containing the stomach, liver, spleen, kidneys, bladder, intestines, and reproductive tract.

'abdominal wall (abdominal walls)' --
the thin muscular wall surrounding the abdominal cavity.

'abraded' --
the external covering or layer of a part is rubbed or scraped.

'acquired lesion (acquired lesions)' --
an injury caused by an agent outside the body.

'afterbirth (afterbirths)' --
the placenta and fetal membranes delivered from the uterus following birth of a calf.

'alveolar capillary (alveolar capillaries)' --
the blood capillary (minute tube) that surrounds the alveoli in the lungs.

'alveolar wall (alveolar walls)' --
the thin wall separating the alveolus from the surrounding blood vessel.

'alveolus (alveoli)' --
Minute air-filled sac in the lungs which is surrounded by small blood vessels. There are large numbers of alveoli in each lung and carbon dioxide are exchanged through the thin walls of the alveolus and its surrounding blood vessels.

'alimentary canal' --
the passage in the body that food goes through: it extends from the mouth through the esophagus, stomach, and intestines to the anus.

'amnion' --
thin tough membrane enclosing the fetus and amniotic fluid, the innermost membrane surrounding the fetus.

'amniotic fluid (amniotic fluids) --
fluid contained in the amniotic sac.

'amniotic sac (amniotic sacs)' -- see amnion.

'anal area (anal areas)' --
an area around or situated near the anus.

'anus (anuses)' --
the opening of the alimentary canal to the exterior through which the undigested remains of food (feces) are passed.

'anterior' --
towards the head end of the body.

'anteriorly' --
in a forward direction, directed toward the head.

'apical lobe of lung (apical lobes of lungs)' --
the anterior lobe is the smallest lobe of the lungs.

'approximated' --
adjoining or side by side.

'articulated' --
bones joined together by tendons and ligaments.

'aspiration (aspirations)' --
the act of inhaling (meconium aspiration - aspiration of meconium by the fetus or newborn which may result in atelectasis or pneumonia).

'atelactasis' --
the failure of fetal lung tissue to convert to air breathing tissue, for detailed explanation refer to text pages.

'atrophy' --
to waste away or to fail to grow.

'autolysis (autolyses)' --
the spontaneous disintegration of tissues or cells by the action of their own autogenous enzymes such as occurs after death and some pathological conditions.

'bacillus (bacilli)' --
any rod-shaped bacterium belonging to the genus Bacillus.

'besnoitiosis' --
is an infection caused by spore forming protozoan of Besnoitia; which characteristically is diagnosed by the gritty feeling of the spore the size of salt grains located on the membranes covering limb bones and tendons.

'biceps femoris' --
a muscle whose action is to extend the hind limb as in propelling the body.

'bladder (bladders)' --
membranous sac into which urine collects and is stored.

'blockage of a bronchus (blockages of bronchi)' --
results from the aspiration of mucus, placental or amniotic fluids.

'brisket (briskets)' --
the lower chest of a quadruped mammal (see Fig. 8).

'bronchial' --
pertains to one or more bronchi, any of the larger air passages of the lungs.

'bronchial obstruction (bronchial obstructions)' --
aspiration of mucus, placental or amniotic fluids or debris blocking the bronchial system.

'bronchiole (bronchioles)' --
one of the finer subdivisions of the branched bronchial system.

'bronchus (bronchi)' --
(1) any of the larger air passages of the lungs.

'brucella (brucellae)' --
a short non-motile microorganism belonging to the family Brucellacease.

'brucellosis' --
a generalized infection of animals or man caused by a species of Brucella.

'canine tooth or canine (canine teeth or canines)' --
the tooth located adjacent to incisors and has a long conical crown.

'canine puncture (canine punctures)' --
bite wound resulting from penetration by the canine teeth.

'carcass (carcasses)' --
a dead body, generally applied to other than a human body.

'carrion' --
dead flesh.

'capillary engorgement (capillary engorgements)' --
local congestion associated with accumulation of blood.

'cerebellum (cerebella or cerebellums)' --
posterior part of the brain consisting of two lateral lobes and a median lobe.

'cerebral cap (cerebral caps)' --
part of skull covering the cerebral hemispheres (see Fig. 10).

'cervical' --
pertaining to the neck, or to the neck of any organ or structure.

'cervical area (cervical areas)' --
pertaining to the neck.

'cervical vertebra (cervical vertebrae)' --
a vertebral bone of the neck (see Fig. 9).

'cervix (cervices)' --
cylindrical (necklike) posterior part of the uterus, which leads to the vagina.

'clostridial' --
pertaining to or caused by clostridia microorganisms of the family Bacillaceae.

'colostrum' --
thin yellow, milky fluid secreted by the udder a few days before or after parturition.

'comatose' --
in a state of coma, loss of consciousness.

'compensatory mortality' -- (in terms of predation)
when an individual killed by a predator would have died from some other cause had the predator not killed it.

'commissure (of the lips)' --
the junction of the upper and lower lips at either side of the mouth (see Fig. 8).

'congenital atelectasis' --
failure to convert fetal to neonatal lung - conditions that are present at birth regardless of their causation.

'congenital form' --
existing at birth, not hereditary.

'contusion (contusions)' --
a bruise or injury of a part without a break in the skin.

'cotelydon (cotelydons)' --
one of the tufted areas of a ruminant's placenta.

'cranial vault - (cranial vaults)' --
part of the skull that encloses the brain and its associated membranes and vessels.

'cranium (craniums or crania)' --
the eight fused bones that form the cranial vault.

'crown of skull (crowns of skulls)' --
the top of the head.

'dental arcade (dental arcades)' --
curving structure formed by the teeth in their normal position
mandibular (lower) arcade - mandibular (lower) teeth
superior dental arcade - maxillary (upper) teeth (see Fig. 10).

'denuded' --
removal of covering by trauma, surgery or pathological change.

'dew claw (dew claws)' --
second and fifth digits of the foot, largely vestigial but more functional in caribou than in other North American cervids (see Fig. 8).

'diaphragm' --
a sheet of tissue, part muscle, part tendon, covered by serous membrane, separating thoracic cavity from abdominal cavity.

'diaphragmatic lobe of lung (diaphragmatic lobes of lungs)' --
the posterior lobe of the lung adjacent to the diaphragm.

'diastema (diastemata)' --
the space between the incisor teeth and the molariform tooth row.

'difused' --
not limited, widely disturbed.

'dilation (dilations)' --
enlargment beyond normal size.

'disarticulated' --
separation or amputation of a bone joint.

'discoloration (discolorations)' --
alteration or change in colour.

'dismembered' --
torn into pieces.

'distended' --
swollen, enlarged, stretched.

'distension (distensions)' --
to swell, enlarge, dilate or inflate.

'dorsal' --
pertaining to the back.

'dorsally' --
pertaining to or on the back of the body.

'dropped' --
to be born.

'duodenum (duodena)' --
the first section of the small intestines between the stomach and the middle portion of the small intestines.

'dystocia' --
a condition resulting from abnormal labour, or due to the size, malpresentation or position of the fetus.

empirical' --
relying or based solely on field observations.

'enucleated' --
removal of an eyeball, organ or tumor without cutting into the flesh.

'Escherchia coli' --
bacteria frequently found in the intestinal tract and may cause intestinal infection.

'esophagus or gullet (esophagi or gullets)' --
the passage for food from the pharynx to the stomach.

'ethmoid bone (ethmoid bones)' --
a cribform or seive-like bone forming part of the nasal cavity.

'expelled' --
eject by force such as muscular contractions.

'expressed' --
squeezed or evacuating by pressure.

'eye socket or orbit (eye sockets or orbits)' --
a bony cavity in the skull into which the eyeball fits.

'fecal' --
pertaining to feces.

'feces' --
undigested remains of food passed out of the body.

'femoral bone (femoral bones)' --
the upper bone in the hind limb extending from the pelvis to the stifle joint (see femur, Fig. 9).

'femur (femurs)' --
the upper bone in the hind limb extending from the pelvis to the stifle joint (see Fig. 9).

'fetal atelectasis' --
the complete failure of fetal lung tissue to convert to air-breathing neonatal lung tissue at birth.

'fetal membranes' --
any one of the membranous structures which surround the embryo during its development period.

'fetus (fetuses)' --
the unborn offspring of mammals.

'flaccid' --
weak, lax, soft, lack of tone.

'flank (flanks)' --
that part of the body posterior to the ribs and anterior to the hip (see Fig. 8).

'flatulence' --
the presence of excessive air or gases in the intestine causing distention.

'focal necrosis' --
a definite area of dead or dying tissues.

'focus (foci)' --
the main centre of a morbid or pathological process.

'foreleg (forelegs)' --
the muscles, ligaments, tendons, and bone of the front leg from the proximal end of the humerus to the distal end of the metacarpus (see Fig. 9).

'fractured' --
the breaking of a bone.

'fracture line (fracture lines)' --
a break or split in a bone.

'fragmentary' --
pieces.

'froth' --
collection of small bubbles.

'gluteus maximus' --
largest of the three rump muscles, which extends the hip joint, one of the main muscles of propulsion.

'gull egestus (gull egesta)' --
indigestible material which is thrown up by a gull.

'head of femur (heads of femurs)' --
approximately hemispherical end of the femur which articulates with the dish-like acetabulum of the pelvis (see Fig. 9).

'heel of the mandible (heels of the mandibles)' --
the curved posterior most lower area of the mandible (see Fig. 10).

'hemorrhage (hemorrhages)' --
the escape of blood from damaged blood vessels - bleeding.

'hemorrhagic' --
descriptive of any tissue into which bleeding has occurred.

'hind leg (hind legs)' --
the muscles, ligaments, tendons, and bones of the back leg from the head of femur to the distal end of the metatarsus (see Fig. 9).

'humeral bone (humeral bones)' --
the humerus or the upper long bone of the upper foreleg (see humerus, Fig. 9).

'humerus (humerii)' --
humeral bone - is the long bone which extends from the shoulder above, where it articulates with the scapula, to the elbow at which it articulates with the radius ulna (see Fig. 9).

'hydrocephaloid or hydrocephalous --
of or like hydrocephalus.

'hydrocephalus' --
abnormal accumulation of fluid in the cranial vault - accompanied by enlargement of the head and prominence of the forehead. It may be congential or acquired.

'hyoid apparatus (hyoid apparatuses)' --
the bone and cartilage structure situated between the vertical parts of the rami of the mandible and supports the tongue, the pharynx and larynx.

'hyoid bone (hyoid bones)' --
a U-shaped movable bone which is the ventral part of the hyoid apparatus and supports the root of the tongue.

'ilium' --
the anterior-most of the three sections of the hip bone.

'incisor tooth or incisor (incisor teeth or incisors)' --
the small spade-like front teeth adapted for cutting, located between the canine teeth in a wolf. Found only in the lower jaw of a caribou, eight in total (see incisor Fig. 10).

'inner canthus (of the eye)' --
the angle at either end of the fissure between the eyelids. Inner or nasal canthus, outer or temporal canthus (see Fig. 8).

'intercostals (intercostal muscles)' --
situated between the ribs, pertaining to muscles or parts between the ribs.

'intestinal tract or intestine (intestinal tracts or intestines)'--
that portion of the alimentary canal extending from the base of the stomach to the anus.

'involuted' --
to return to a normal size after enlargement; the retrograde changes in the female genital organs that result in the return to normal size after delivery.

'kidney (kidneys)' --
two organs in the lumbar area that filter the blood and excrete the end products of body metabolism in the form of urine.

'kidney fat' --
deposition of fat around kidneys, which can be used as an indicator of physical condition.

'larynx (larynxes)' --
the cartilage structure that connects the pharynx and trachea - regulates the volume of air in breathing and contains the vocal cords.

'lateral' --
denotes a position further from the midline of the body.

'laterally' --
pertaining to the side.

'limb (limbs)' --
leg or arm.

'liver (livers)' --
large glandular organ that secretes biles, stores vitamins and minerals and purifies venous blood.

'lobe (lobes)' --
roundish, flattish parts of the liver or rounded major sections of the lungs.

'lobule (lobules)' --
a somewhat rounded projection of division of an organ of the body.

'lumbar area (lumbar areas)' --
is the area between the thoracic vertebrae and the sacrum.

'lumbar fossa area (lumbar fossa areas)' --
trianglular depression on the upper part of the flank, posterior to the last rib.

'lumbar vertebra (lumbar vertebrae)' --
a vertebral bone between the thoracic vertebrae and sacrum (see Fig. 9).

'lung (lungs)' --
the paired organs where gases are exchanged from the air into and from the blood.

'main digit (main digits)' --
(hoof, hooves) third and fourth digits of the foot that provide the primary support (see Fig. 8).

'malnutrition/starvation complex' --
results from an unbalanced or insufficient diet or deprivation of food.

'mandible (mandibles)' --
is the lower jaw bone in vertebrates which is the largest bone of the face and carries the lower teeth (see Fig. 10).

'mandibular bone (mandibular bones)' --
pertaining to the mandible (see mandible, Fig. 10).

'mandibular symphysis (mandibular symphyses)' --
the joint between the anterior end of the left and right mandible.

'marrow fat' --
soft organic material that fills the cavities of bones, whose fat content is used as an indication of physical condition.

'maxilla (maxillae)' --
an irregular shaped bone that forms the upper jaw, assists in the formation of the eye socket, nasal cavity and palate, and lodges the upper teeth (see Fig. 10).

'maxillary bone (maxillary bones)' --
one of the bones of the upper jaw that carries all the upper teeth except the incisors. (see maxilla, Fig. 10).

'meconium' --
a dark green mucilagenous material in the intestine of the full term fetus.

'membrane (membranes)' --
a thin, soft, piable sheet or layer of tissue.

'mesenteric' --
pertaining to the mesentery: the membranous peritoneal fold attaching various organs to the abdominal wall.

'metacarpus (metacarpii)' --
(metacarpal bone, metacarpal bones) the third and most distal of the long bones in the foreleg (see Fig. 9).

'metatarsus (metatarsii)' --
(metatarsal bone, metatarsal bones) the third and most distal of the long bones in the hind leg (see Fig. 9).

'metritis' --
inflamation of the uterus.

'microscopically' --
of extremely small size, visible only with the aid of a microscope.

'milk curd (milk curds)' --
milk coagulated by the stomach juices.

'mucous' --
of, containing, or secreting mucus.

'mucous membrane (mucous membrances)' --
the lining of all cavities of the body which open externally, such as the mouth, nose, intestines and which secrete mucus.

'mucus (mucuses)' --
free slime from the mucous membranes.

'muscle mass (muscle masses)' --
highly specialized organs which by contraction produce movement.

'muscle tone' --
resistance to passive elongation or stretch, lack of muscle tone usually means a lack of muscle exercise.

'muscular dystrophy' --
a degenerative myopathy characterized by weakness and atrophy of muscle.

'nasal (nasals)' --
pertaining to the nose.

'nasal bone (nasal bones)' --
one of the bones of the face; forming the greater part of the roof of the nasal cavity (see Fig. 10).

'nasal passage (nasal passages)' --
a longitudinal cavity extending through the upper part of the face and divided by a median septum (wall) into right and left halves (see Fig. 10).

'necropsy (necropsies)' --
autopsy, examination of a body after death.

'necrosis (necroses)' --
death of tissue.

'necrotic patch (necrotic patches)' --
area of tissue necrosis.

'neonatal atelectasis' --
imperfect expansion of lungs immediately after birth.

'neonate (neonates)' --
newly born.

'nostril (nostrils)' --
one of the extenal orifices of the nose through which the animal breathes (see Fig. 8).

'nutrition' --
the processes involved in taking in food nutrients and assimilating and utilizing them.

'nucleus (nuclei)' --
a spheroid body within a cell, visible with a light microscope.

'orbit (orbits)' --
bony cavity which contains the eyeball (see Fig. 10).

'paralumbar' --
pertains to paralumbar fossa area.

'paralumbar fossa (paralumbar fossae)' --
triangular depression on the upper part of the flank, anterior to the last rib (see Fig. 8).

'paralumbar fossa area (paralumbar fossa areas)' --
triangular depression on the upper part of the flank, anterior to the last rib (see Fig. 8).

'parturiency (state of)' --
pertaining to giving birth, the condition of being parturient.

'parturient' --
give birth or about to give birth.

'pathogenesis (pathogeneses)' --
the development of a disease.

'patho-physiological' --
a death category used in this report that included all pathological or physiological disorders not placed in specific categories.

'pedestal (pedestals)' --
the projection of parietal bone on the skull that supports the antlers (see Fig. 9).

'pelage (pelages)' --
hairy or wooly coat of mammals.

'pelvis (pelves)' --
the posterior part of the abdomen surrounded by the pelvic girdle (pelvic cavity).

'pelvic girdle (pelvic girdles)' --
the bones supporting the hind legs, and the associated tissues (see Fig. 9).

'penetration (penetrations)' --
the act of piercing.

'perforation (perforations)' --
the act of boring or piercing through a part.

'pericardial sac (pericardial sacs)' --
the fibroserous (thin, fibrous) sac that surrounds the heart.

'peritoneum' --
the transparent, thin membrane lining the abdominal cavity.

'peritonitis' --
inflamation of the peritoneum marked by exudation of serum, fibrin, cells and pus.

'phagocytic cell (phagocytic cells)' --
any cell that ingests micro organisms or other cells and foreign particles.

'pharynx' --
the muscular and membranous cavity of the alimentary canal leading from the mouth and nasal passages to the larynx and esophagus.

'placenta' --
the vascular organ that links the fetus to the maternal blood system and which attaches the fetus to the uterine wall.

'placental fluid (placental fluids)' --
those fluids surrounding the amniotic sac enclosing the fetus.

'placental tissue (placental tissues)' --
the cells and cell products that form the placenta.

'pneumonia' --
a disease of the lungs in which the tissue becomes inflamed with copious exudate filling the alveoli.

'posterior' --
towards the rear.

'post-mortem' --
occurring or performed after death.

'predation' --
the killing and eating.

'predator (predators)' --
an animal that preys (kills) and feeds.

'predisposed' --
a tendency or a susceptibility to disease.

'prey' --
the victim of predation.

'prolapse' --
the protrusion of the uterus through the vaginal orifice.

'prolapsed uterus (prolapsed uterii)' --
protrusion of the uterus through the vaginal orifice.

'proximal cause (proximal causes)' --
nearest or closest to any point of reference.

'puncture (punctures)' --
the act of piercing or penetrating with a pointed object.

'putrefactive tissue (putrefactive tissues)' --
the enzymatic decomposition, especially proteins with the production of foul smelling compounds.

'pyelonephritis' --
the inflamation of the kidney from bacterial infection.

'quadrant (quadrants)' --
any one of four corresponding parts or quarters.

'qualified' --
limited or modified in some way.

'quantified' --
determined, expressed or measured quantity.

'radius-ulna' --
the second long bone of the foreleg, formed by the larger radial bone and the smaller ulnar bone, distal to the humerus and proximal to the metacarpus (see (Fig. 9).

'ramus (ramii)' --
another term for the mandibular bone (see mandible, Fig. 10).

'rib (ribs)' --
any of paired elastic arches of bone extending from the thoracic vertebrae (see Fig. 9).

'rib cage (rib cages)' --
bony structure formed by the ribs ventrally united by the sternum enclosing the thorax (see Fig. 9).

'rump' --
the buttocks, the hind part of the body where the legs and the back come together (see Fig. 8).

'rupture' --
to burst or break a cell, vessel or membrane.

'sacrum (sacrums)' --
a thick triangular bone at the posterior end of the spinal column where it forms the dorsal part of the pelvic girdle (see Fig. 9).

'scapula (scapulae)' --
shoulder blade (scapula bone) - a flat triangular shaped bone in the shoulder (see Fig. 9).

'scapular blade (scapular blades)' --
flat part of scapula (see scapula, Fig. 9).

'scapulo-humeral joint (scapulo-hemeral joints)' --
shoulder joint - its chief movements are flexion and extension of the forelegs (see Fig. 9).

'scavenge' --
the eating of refuse or dead or decaying flesh.

'scavenger (scavengers)' --
an animal that eats refuse or dead or decaying flesh.

'scours' --
diarrhea or dysentry, especially in newborn animals.

'serous membrane' --
a thin layer of tissue which covers an organ or lines a cavity.

'serum' --
the clear liquid which separates in the clotting process from the clot forming parts of the blood.

'shoulder (shoulders)' --
the lateral part of the body overlying the scapula area and forming the connection of the foreleg to the torso (see Fig. 9).

'skull (skulls)' --
the bony framework of the head (see Fig. 10).

'skull cap (skull caps)' --
dome like upper portion of the cranium (see Fig. 10).

'spinal column (spinal colums)' --
the spine which is the series of vertebrae that form the backbone (see vertebral column, Fig. 9).

'spinal process (spinal processes)' --
prominence or projection from vertebrae of the spinal column (see Fig. 9).

'spleen (spleens)' --
organ that produces and stores certain constituents of the blood.

'sternal joint (sternal joints)' --
the joints formed by the articulation of the ribs with the sternum.

'sternum (sternums)' --
longitudinal unpaired plate of bone (breast bone) which forms the ventral wall of the thorax, with which most of the ribs ventrally articulate (see Fig. 9).

'stifle (stifles)' --
corresponds to the knee joint in the human (see Fig. 8).

'stillbirth (stillbirths)' --
the birth of a stillborn (dead when born).

'stomach (stomachs)' --
The musculomembranous expansion of the alimentary canal between the eosophagus and the duodenum.

'thoracic area (thoracic areas)' --
in the area of the thorax.

'thoracic cavity (thoracic cavities)' --
is the second largest body cavity, which contains the lungs and heart.

'thoracic vertebra (thoracic vertebrae)' --
the vertebral bones associated with the chest and ribs (see Fig. 9).

'thorax (thoraxes)' --
that part of the body between the neck and the diaphragm encased by the ribs (see Fig. 8).

'tibia-fibula' --
the second long bone of the hind leg, formed by the larger tibial bone and the smaller fibular bone, distal to the femur and proximal to the metatarsus (see Fig. 9).

'tooth puncture (tooth punctures)' --
a hole made by a sharp tooth (e.g. wolf canines).

'torso (torsos)' --
the body trunk which is the body excluding the head and limbs.

'trachea (trachae)'
a cartilagenous and membranous tube descending from the larynx and branching into the right and left main bronchi.

'trauma (tramata or traumas)' --
a wound or injury.

'traumatic' --
pertaining to, occurring as a result of a trauma.

'traumatized' --
to damage tissues by force, or by chemicals or by other agents.

'turbinate (turbinates)' --
the turbinate bones are delicate scroll-like bones which project into the nasal passage.

'udder (udders)' --
mammary gland located on the ventral abdomen between the hind limbs.

'umbilical cord (umbilical cords)' --
a flexible structure connecting the umbilicus with the placenta.

'umbilical stump (umbilical stumps)' --
remnant of umbilical cord attached to newborn.

'umbilicus (umblilici)' --
the navel site of attachment of the umbilical cord to the fetus.

'undiscerned' --
not determined or not detected.

'untypical' or 'atypical' --
irregular; not conformable to type.

'urethra (urethrae)' --
the membranous canal conveying the urine from the bladder to the exterior of the body.

'uterine tissue (uterine tissues)' --
pertaining to the tissues forming the uterus.

'uterus (uterii)' --
hollow muscular organ in female animals in which the fetus is nourished.

'vagina (vaginas or vaginae), --
a canal in the female extending from the vulva to the cervix.

'vaginal orifice (vaginal orifices)' --
entrance to the vagina.

'viscera' --
the organs found in any of the three body cavities, especially those of the abdominal cavity.

'vulva' --
the region of the external genital organs of the female.

'ventral' --
located near or on a lower surface.

'ventrally' --
toward the underside (belly).

'vertebral column (vertebral columns)' --
the assemblage of vertebrae which are individual bones through which the spinal cord runs (see Fig. 9).

'withers' --
top of the shoulders (see Fig. 8).

'xyphoid cartilage (xiphoid cartilages)' --
cartilagenous posterior extension of the sternum.

Appendix 5

An approximate evaluation of helicopter searching effort for dead caribou, Beverly calving ground, Northwest Territories, 1981-83

Date	Hours flown	Number of carcasses found	Minutes flown/ carcass
1981			
31 May	2.3	2	69
1 June	1.6	1	96
2	-[a]	-	-
3	3.5	3[b]	70
4	3.0	3	60
5	-	-	-
6	2.8	6	28
7	3.6	6	36
8	4.0	9	27
9	1.4	2	42
10	2.3	6	23
11	-	-	-
12	-	-	-
13	-	-	-
14	3.4	4[c]	51
15	2.6	5[b]	31
16	-	-	-
17	4.6	6	46
18	0.5	2	15
19	5.9	13	27
20	3.3	10[b]	20
21	-	-	-
22	-	-	-
23	-	-	-
1982			
31 May	-	-	-
1 June	-	-	-
2	-	-	-
3	-	-	-
4	-	-	-
5	-	-	-
6	-	-	-
7	-	-	-
8	3.0	3	60
9	5.4	9	36
10	-	-	-
11	2.4	3	48
12	3.0	-	-

Appendix 5 (cont'd)

Date	Hours flown	Number of carcasses found	Minutes flown/ carcass
1982 (cont'd)			
13	3.0	2	90
14	2.1	5[d]	25
15	3.0	10	18
16	3.8	10	23
17	6.3	43	9
18	4.0	13	18
19	–	–	–
20	–	–	–
21	–	–	–
22	–[b]	2	–[b]
23	4.0	4	60
1983			
31 May	–	–	–
1 June	–	–	–
2	–	–	–
3	–	–	–
4	–	–	–
5	–	–	–
6	3.5	3	70
7	4.8	3	96
8	0.5	1	30
9	–	–	–
10	5.0	6	50
11	5.0	13	23
12	4.7	7	40
13	5.4	11	24
14	–	–	–
15	5.6	11	30
16	4.7	22	13
17	5.9	35	10
18	–	–	–
19	–	–	–
20	–	–	–
21	–	–	–
22	–	–	–
23	–	–	–

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[a] No helicopter searching occurred on these dates.

[b] One calf found by ground observers.

[c] Three calf carcasses and one cow carcass found by ground observers.

[d] Eight calf carcasses found by ground observers.